Are seabirds breeding in the southeastern Bering Sea food-limited?

Final Report to the
North Pacific Marine Research Program

Project Title: Effects of food stress on reproductive performance of seabirds at Pribilof and Bogoslof Islands

Alexander S. Kitaysky[1], John F. Piatt[2], and John C. Wingfield[1]

[1]Zoology Department, University of Washington Box 315800, Seattle, WA 98020
[2]Alaska Science Center, USGS, 1011 E. Tudor Rd., Anchorage, AK 99503

October 2002

SUMMARY
During the past three decades, populations of some seabirds declined in the Bering Sea perhaps because of a decline in food availability or abundance of high-quality forage fish. To test a hypothesis that seabirds in the southeastern Bering Sea are food-limited during the reproductive season, we applied a field endocrinology technique that directly relates the physiological condition of seabirds to variations in food availability. In particular, concentrations of the stress hormone corticosterone in the blood of undisturbed seabirds (baseline levels) reflect current foraging conditions, and the rise in blood levels of corticosterone in response to a standardized stressor of capture, handling and restraint (maximum acute stress induced levels) reflect recent nutritional history.

We applied these techniques to kittiwakes (*Rissa* spp.) and murres (*Uria* spp.) breeding on St. Paul and St. George Islands (Pribilofs, declining populations) and Bogoslof Island (increasing populations). We found that, during 1999, common murres (*U. aalge*) and black-legged (*R. tridactyla*) kittiwakes breeding in the southeastern Bering Sea experienced food-shortages, as evidenced in their increased levels of corticosterone relative to those in seabirds breeding in food-rich areas of the Gulf of Alaska. Also, birds breeding on the Pribilofs were more affected by food shortages compared to birds breeding on Bogoslof I.: parent thick-billed murres (*U. lomvia*) and red-legged kittiwakes (*R. brevirostris*) at St. George I., and common murres and black-legged kittiwakes at St. Paul I. were in poorer physiological condition compared to con-specifics breeding on Bogoslof I. Similarly in 2000, elevated corticosterone levels indicated that foraging conditions for black-legged kittiwakes breeding on St. George I. and common murres breeding on St. Paul I. were less favorable than for their con-specifics breeding on Bogoslof I. In 2000, seabirds breeding on Pribilof and Bogoslof Islands were food-limited at the beginning of reproductive season, but were not food-limited during mid- to late-summer. Reproductive performances of black- and red-legged kittiwakes, and common murres, were negatively correlated with corticosterone levels at the late-incubation and early chick-rearing stages of reproduction. For red-legged kittiwakes and thick-billed murres, corticosterone levels were also correlated with diet quality, as determined from fatty acid analyses of the adipose tissue; an increased adrenocortical response to acute stress was associated with diets low in lipids. We conclude that food availability during early stages of reproduction (likely during arrival of seabirds at breeding colonies) was a factor that limited reproductive performance of seabirds in the south-eastern Bering Sea in 1999 and 2000. Birds nesting on the Pribilofs were affected more severely than their con-specifics nesting on Bogoslof I. These results support our original hypothesis that seabird population trends in the south-eastern Bering Sea were related to food supplies during reproduction.

We also examined stress status, and the behavioral and physiological consequences of food-related stress in young seabirds. Chronically elevated corticosterone levels were documented in captive individuals reared on low-quality and/or reduced-quantity food. We established empirical relationships between daily energy intake and corticosterone levels in kittiwake and common murre chicks. Based on these empirical relationships, we found that in 2000, chicks of red-legged and black-legged kittiwakes breeding on St. George I. were experiencing nutritional deficit, whereas chicks of black-legged kittiwakes breeding on St. Paul I. and chicks of murres breeding on Bogoslof I. were not food-limited. Finally, our study of captive red-legged kittiwakes provided evidence that even a short episode of nutritional stress during development has long-lasting detrimental effects on birds' foraging efficiency. Reduced

foraging abilities are likely to translate into a decreased survival and reduced fitness of affected individuals that in turn would further exacerbate declines of seabird populations.

The research presented here was a component of a multi-disciplinary research program entitled "Regime Forcing and Ecosystem Responses in the Bering Sea" (ReFER), which included two other projects that focused on the biological responses of seabirds to variations in their environments. Specifically, this project was conducted in a close coordination with the project titled "Seabird monitoring" (PI – Vernon Byrd, Alaska Maritime National Wildlife Refuge), which was responsible for logistics on the Pribilof and Bogoslof islands and collection of data on breeding biology of birds. This study was also coordinated with the project titled "Estimating Seabird Diets Using Fatty Acids: Protocol Development and Testing of ReFER Hypotheses" (PIs – Sara Iverson and Alan Springer); and with projects on seabird-forage fish interactions supported by the Exxon Valdez Oil Spill Trustees and US Geological Survey in Cook Inlet.

The data from the project are summarized here and are parts of more detailed reports (Kitaysky et al. 2001a [attached]; Wingfield and Kitaysky *in press*; Benowitz-Fredericks and Kitaysky *in prep.* [attached]; and Kitaysky et al. *in prep.* [attached]). Data collected from captive birds were also used in the final report for the "Estimating Seabird Diets Using Fatty Acids: Protocol Development and Testing of ReFER Hypotheses" component of ReFER.

A. INTRODUCTION

During the past three decades, population declines have occurred among some seabird and marine mammal species in the southeastern Bering Sea and Gulf of Alaska. It has been suggested that declines in food availability or in the abundance of high-quality forage fish resulted in food-related stress (Merrick *et al*. 1987, Hunt et al. 1996, Piatt & Anderson 1996), which in turn reduced reproductive success of marine top-predators. In this context, nutritional stress can be defined as changes in the physiological condition of individuals that experience a shortage of food that impairs their ability to reproduce successfully. Alternatively, less severe food shortages may allow reproduction to proceed, but low post-fledging survival of young raised on low quality diets may precipitate reproductive failure. Prior to this study there was no direct evidence that seabirds breeding in the south-eastern Bering Sea were nutritionally stressed. Here we examine temporal and spatial variability in physiological condition of seabirds in the south-eastern Bering Sea to assess whether they experienced food-related stress during reproductive seasons of 1999-2000.

Traditional methods of detecting food-related stress in populations of free-living marine top-predators are not always effective. In long-lived seabirds, fluctuations in food resources during reproduction should affect reproductive success, or the survival of young, rather than survival of adults. Consequently, survival of chicks in the nest is commonly used to assess effects of food shortages on reproductive performance of seabirds (e.g., Kitaysky and Golubova 2000). However, survival of seabird chicks may be affected by factors which are independent of food supplies, such as predation and inclement weather (e. g., Lloyd 1979). On the other hand, when food shortages occur, several factors might mask effects of food-related stress on survival of chicks. In some seabirds, chicks may tolerate large fluctuations in food supply and fledge successfully despite food shortages (? yan and Anker-Nilssen 1996; Kitaysky 1999). In other

species, parents buffer their young from variations in food availability by increasing their effort in foraging during food shortages (Shea and Ricklefs 1995, 1996; Zador and Piatt 1999; Kitaysky et al. 2000). Post-fledging survival of young and their recruitment into breeding populations may also reflect foraging conditions and/or nutritional history of recruits during their development in the nest (Thompson and Ollason 2001; Kitaysky et al., in press). For instance, in the common murre, population declines on food-poor colonies in Cook Inlet coincided with high reproductive success, determined as the proportion of chicks that survive until fledging (Piatt 2002). Similarly, population declines of red-legged kittiwakes at the Pribilofs during the early 1980s probably resulted from a decreased post-fledging survival of kittiwakes born during the late 1970s rather than a decreased production of chicks (Hunt and Byrd 1999).

Thus, the question arises as to whether birds breeding in the southeastern Bering Sea are food-limited during the breeding season. To answer this question, we applied an additional tool that directly measures nutritional stress in free-living seabirds. In particular, concentrations of the stress hormone corticosterone in the blood of undisturbed seabirds (baseline levels) reflect current foraging conditions, and the rise in blood levels of corticosterone (acute stress induced levels) in response to a standardized stressor (capture, handling and restraint) reflect recent nutritional history. Baseline level is defined by the concentration of corticosterone circulating in the blood of free-ranging animals. It is often elevated in animals that suffer current effects of food deprivation, and can only be measured in blood collected immediately (usually within 3 min) after capture; i.e., before corticosterone levels rise in rapid response to the additional acute stress of capture and restraint. However, this acute stress-induced adrenocortical response to capture and handling also offers insight into historical levels of food-related stress (e.g. within past few weeks) because steroidogenic cells of the adrenal glands change their sensitivity and/or capacity for corticosterone secretion in response to prolonged food shortages (e.g. Kitaysky et al. 1999b, 2001a and references therein). Thus, measures of baseline and acute stress-induced levels of corticosterone allow us to distinguish between current and historical foraging conditions in free-living seabirds. We applied these techniques to seabirds breeding in the south-eastern Bering Sea to assess whether seabirds breeding on the Pribilof Islands (declining population trends) and Bogoslof I. (increasing population trends) are food-limited.

In previous work, we determined how seabird reproductive biology and behavior varied with food supplies (Piatt 2002). We also established functional relationships among corticosterone levels, food availability and reproductive performances. In adult seabirds, corticosterone levels were elevated in black-legged kittiwakes and common murres breeding when food was in short supply (Kitaysky et al. 1999a; Wingfield and Kitaysky, in press; Kitaysky et al. in preparation). Experimental studies of free-living black-legged kittiwakes indicated that increased levels of corticosterone could result in a reduced reproductive performance and decreased post-breeding survival of affected individuals (Kitaysky et al. 2001b). A long-term study of seabirds breeding in Cook Inlet has revealed a direct relationship among corticosterone levels, food abundance, reproductive performance and persistence of individuals in populations (Kitaysky, Piatt and Wingfield, in preparation). This provides data for calibration of relationships between food supply and stress hormones in seabirds, and allows us to assess foraging conditions for seabirds breeding in the Bering Sea in absence of independent data on availability of their food. For example, baseline levels of corticosterone in common murres were negatively correlated with current food abundance (Fig. 1A), whereas acute stress-induced levels of corticosterone were negatively correlated with prior food abundance (Fig. 1B).

Corticosterone levels were also negatively correlated with reproductive performance (Fig. 2), and baseline levels predicted persistence of adult individuals affected by food shortages in a population (Fig. 3). Breeding adults were more likely to disappear between years, or skip breeding, when their corticosterone levels were elevated.

Fig. 1. The relationship between current (**A**) and former (**B**) food abundance and concentrations of corticosterone in Common Murres breeding on Duck (D) and Gull (G) islands in Cook Inlet, Alaska. (From Kitaysky et al., in prep).

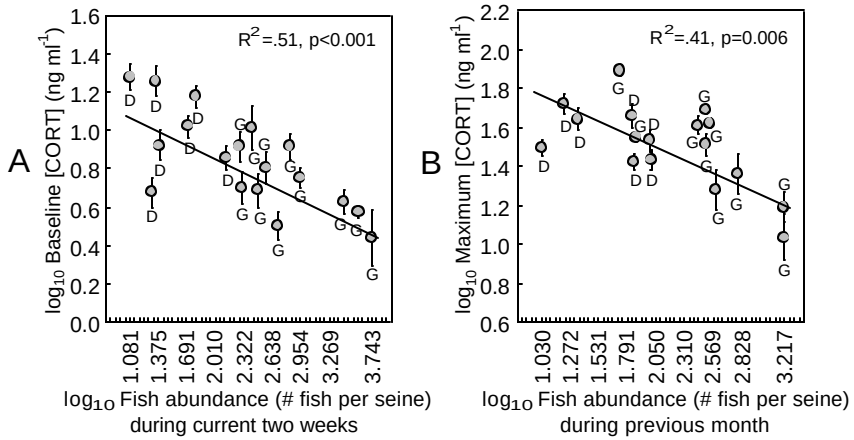


Fig. 2. Corticosterone levels in incubating common murres (Cook Inlet, 1997-2000) as a predictor of their success in hatching of chicks (A), and overall productivity (B). (From Kitaysky et al., in prep).

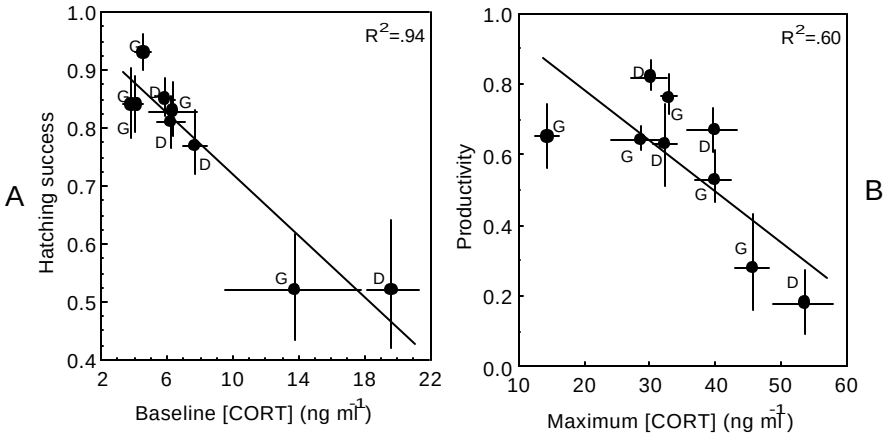
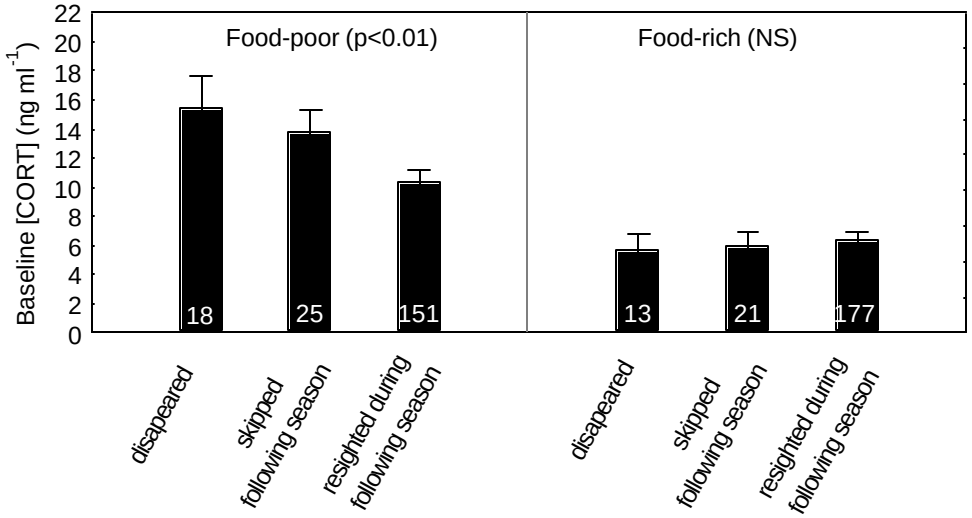


Fig. 3. The relationship between baseline corticosterone levels and persistence of adult common murres in the food-rich vs. food-poor environments (from Kitaysky et al., in prep).



We have also been investigating the mechanisms by which food-related stress translates into reduced fitness. Chronically elevated corticosterone levels were documented in black-legged kittiwake chicks individuals reared on low-quality and/or reduced-quantity food (Kitaysky et al. 1999b). Chronically elevated corticosteroid levels are known to result in suppression of memory and immune systems, lead to muscle wasting and cause neuronal cell death (e.g. Sapolsky 1987; also reviewed in Wingfield 1994). Recent studies of young black-legged kittiwakes provided evidence that even a short episode of exposure to experimentally elevated levels of corticosterone during development might have a long-lasting detrimental effect on a bird's foraging efficiency (Kitaysky et al., in press). Thus, exposure to poor quality of food and/or decreased food availability during development might have similar debilitative effects on foraging efficiency of young seabirds in the wild. Reduced foraging abilities are likely to translate into a decreased post-fledging survival and reduced fitness of birds that in turn would further accelerate declines of seabird populations. However, an empirical relationship between daily energy intake and corticosterone levels in chicks of other seabirds (except black-legged kittiwakes) has not been previously established. Furthermore, it was not known whether an episode of food-stress during development would result in effects similar to debilitative effects of exogenous corticosterone on cognitive abilities of individuals.

In summary, the results of our previous studies of seabird stress physiology provided a background to investigate the potential for food-related stress in seabirds breeding in the south-eastern Bering Sea in 1999 and 2000. In this study, we focused on the comparison of endocrinological characteristics of black-legged and red-legged kittiwakes, and common and thick-billed murres breeding at Bogoslof Island, where foraging conditions were assumed to be good during the last few years, with those nesting under potentially poor feeding conditions at the Pribilof Islands. We also conducted experiments on captive birds to establish effects of food-related stress on corticosterone levels in common murre and red-legged kittiwake chicks, and on cognitive abilities of individuals later in life.

B. OBJECTIVES

1. Establish whether red-legged kittiwakes, black-legged kittiwakes, common murres and thick-billed murres breeding at Pribilof and Bogoslof Islands are food-stressed: (A) Assess inter-annual and intra-seasonal variability of corticosterone levels in birds breeding on St. Paul, St. George and Bogoslof Islands; and (B) Compare physiological parameters of common murres and black-legged kittiwakes breeding in the south-eastern Bering Sea (food abundance has not been measured independently) with those of con-specifics breeding in Cook Inlet (food abundance has been measured independently); (C) Examine the relationships among corticosterone levels, behavior and reproductive performance.
2. Examine the effects of variation in daily energy intake and quality of food on baseline levels of corticosterone in red-legged kittiwake and common murre chicks. Determine the effects of food-related stress on morphological development and rate of corticosterone secretion of captive chicks.
3. Examine effects of an episode of nutritional stress during development on quality of red-legged kittiwakes later in life.

C. METHODS

The field studies were conducted on St. George and St. Paul Islands (Pribilofs) and on Bogoslof Island in late-July and early August of 1999 and during June – August in 2000. A total of 147 red-legged kittiwakes, 146 black-legged kittiwakes, 142 common murres and 176 thick-billed murres were sampled for stress hormones in the wild. Laboratory analyses and captive-rearing, learning, and foraging efficiency trials were conducted at the University of Washington. Collections of field samples and experimental manipulations have been carried out according to federal and state collection permits and University of Washington Animal Use and Care Committee protocols.

1. *Body condition and Corticosterone levels in free-ranging seabirds.*

To assess whether seabirds from the different populations were food-limited or not, we measured corticosterone in seabirds at different stages of reproduction from early-incubation to chick-rearing. Adult birds were captured with a noose pole at their nests, chicks were taken directly from their nests and murre fledglings were captured during travel from their nests to the ocean. All birds were bled according to previously established protocols (for details see Kitaysky et al. 1999a, b; 2001a, b). In brief, all birds were bled according to the following standardized technique: an initial sample was collected within three minutes after capture, and further samples were taken at 10, 30, and 50 minutes. Initial blood samples were considered to reflect baseline levels of corticosterone because corticosterone levels generally do not start to increase until 3 min after capturing (Wingfield and Farner 1976), and in this study we also did not find a significant relationship between time after capture (within 0-3 minutes interval) and concentration of corticosterone. After each sample, blood flow was stopped by application of cotton and birds were placed in individual opaque cloth bags. After collection of blood, hematocrit tubes were emptied into 0.5 ml vials, which were stored on ice. Within 12 hours, blood samples were centrifuged and plasma collected. Plasma samples were frozen at -20°C and transported to the University of Washington for radioimmunoassay analyses.

Captured birds were weighed, measured for wing chord, bill and tarsus length, and banded with a standard aluminum band between subsequent bleeds. After sampling, birds were released at the colony (adults and fledglings) or placed back in their nests (chicks). In most cases adults resumed their parental duties 1-10 minutes after they were released. Earlier studies did not find sex-dependent differences in baseline and stress-induced levels of corticosterone in the black-legged kittiwake and common murre (Kitaysky et al. unpublished), thus sex of birds was ignored in this study. No birds were sampled more than once during the season, and all collections of blood samples occurred during day-light hours.

The ratio of body mass to wing chord, bill or tarsus length provides a size-independent index that is commonly used to assess body condition (as a measure of endogenous fat reserves) in birds. However, we found that length of wing chord in black-legged kittiwakes decreases significantly during the breeding season owing to wear on tips of the primaries. Consequently bill and tarsus length were used to estimate body condition index, which we calculated as a ratio of body mass (g) to (bill length + tarsus length) (mm).

Inter-annual and intra-seasonal changes of body condition, baseline levels of corticosterone and acute stress-induced levels of corticosterone (expressed as a maximal level of corticosterone achieved during 50 min of restraint) were examined with analyses of variance (ANOVA, or its non-parametric equivalents), where year, colony and reproductive stage were used as factors. For multiple comparisons of the means we used LSD and Tukey post-hoc tests. Linear regression analyses were used to examine the relationship between diet quality (as determined with QFASA analyses of fatty acid composition, for details of the method and results see Iverson and Springer ReFER report), reproductive performance (for details and results see Byrd ReFER report) and corticosterone levels.

Colony attendance and chick provisioning were determined from all-day (14-hr) continuous observations of a plot of 8-13 nest sites at each study location. The time of adult arrivals, delivery of food to chicks, exchanges of brooding duties and adult departures were recorded. Loafing time was calculated as per cent time both parents were simultaneously present at the nest. Time chicks spent alone was calculated as per cent time chicks spent un-attended by parents. Foraging trip duration was calculated for complete trips only; trips that were in progress when the observation period started/ended were not included. Frequency of foraging trips was calculated only for trips that ended with chick provisioning. When possible, colony attendance data collected in 2000 were compared to data available for the same species/location from earlier studies (as reported in Kitaysky et al. 2000). During analyses, we used nest site as the sampling unit.

2. *Captive study of the effects of food-related stress.*

To test whether the food-related stress affects behavior, morphological development and physiological condition of young seabirds, we raised red-legged kittiwake and common murre chicks on different nutritional regimes in captivity according to already established protocols (for the details of experimental manipulations see attached manuscripts). In brief, young were raised on different quantities of high quality (silverside *Menidia menidia*) and low quality (rainbow smelt, *Osmerus mordax*) food. Chick measurements, collection of blood samples and behavioral trials testing foraging efficiency and learning abilities of experimental birds were carried out according to standardized protocols (for details see Kitaysky et al. 1999b, 2001, *in press*).

3. *Laboratory analyses*

In parallel with the field and captive research, we conducted laboratory analyses of blood samples taken from the birds during the experimental manipulations. All blood samples were taken from the brachial vein of the wing; blood plasma were separated from blood cells and then frozen at -10^{o}C. All plasma samples were transported to the University of Washington and processed according to the radio-immunoassay protocols (for a detailed description of the analysis see Wingfield & Farner 1975, Wingfield *et al*. 1992). In brief, corticosterone concentrations were measured in duplicate for each sample after extraction in dichloromethane. Recovery values following extraction ranged from (80 to 90%) were used to adjust assayed concentrations of corticosterone. Intra- and inter-assay coefficients of variation were 4% and 6%, respectively.

D. RESULTS AND CONCLUSIONS

COMMON MURRES

INTER-ANNUAL COMPARISONS

Body condition

Body condition (Fig. 4) of adult common murres at late-incubation – early chick-rearing did not differ between colonies (colony effect: $F_{1, 77}$=0.32, p=0.576). However, there was a significant interaction between year and colony ($F_{1, 77}$=8.31, p=0.005), indicating that body condition of birds at Bogoslof I. didn't change between 1999 and 2000, whereas birds breeding at St. George I. in 1999 were significantly lighter than in 2000 (Fig. 4). Body condition of birds at St. Paul I. was assessed only in 2000, and it was similar to body condition of birds at St. George I. in 1999 (Fig. 4).

Baseline levels of corticosterone

Baseline levels of corticosterone in parent murres during late-incubation – early chick-rearing did not differ between colonies (colony effect: $F_{1, 69}$=0.59, p=0.446, Fig. 5). However, there was a significant interaction between year and colony ($F_{1, 69}$=4.34, p=0.041), indicating that baseline levels of corticosterone in birds nesting at Bogoslof Island didn't change between 1999 and 2000, whereas birds breeding at St. George I. in 1999 had significantly higher levels than in 2000. Baseline levels of corticosterone in birds at St. Paul I. were assessed only in 2000, and they were similar to baseline levels in birds at St. George I. in 1999 and at Bogoslof in 1999 and 2000 (Fig. 4).

Adrenocortical response to acute stress

Maximum levels of corticosterone (Fig. 4) achieved by common murres in response to acute stress of capture and restraint were significantly higher in 1999 than in 2000 (year effect: $F_{1, 63}$=9.34, p=0.003), and this trend was similar between the colonies (colony X year interaction: $F_{1,}$

$_{63}$=1.11, p=0.296). Maximum levels of corticosterone in birds at St. Paul I. were assessed only in 2000, and they were elevated compared to those in birds at Bogoslof I. and St. George I. in 2000.

Maximum levels of corticosterone in individual murres at incubation were significantly negatively correlated with fledging success (beta=-0.54, R^2=.30, $F_{1, 51}$=21.38, p<0.00003, Fig. 5), and productivity (beta=-0.45, R^2=.20, $F_{1, 51}$=12.72, p<0.001) determined colony-wise (see V. Byrd ReFER report for details). During late-incubation – early chick-rearing, maximum levels of corticosterone achieved by common murres were significantly negatively correlated (beta= -.28, R^2=.08, $F_{1, 51}$=21.38, p=0.042) with the proportion of lipids in the colony/year/month-specific diets (as estimated from fatty acids composition of adipose tissue (QFASA model), see A. Springer and S. Iverson ReFER report for Methods and Results).

Fig. 4. Inter-annual and inter-colony variability of physiological parameters in adult common murres during late-incubation - early chick-rearing, Bering Sea 1999-2000 (mean, SE).

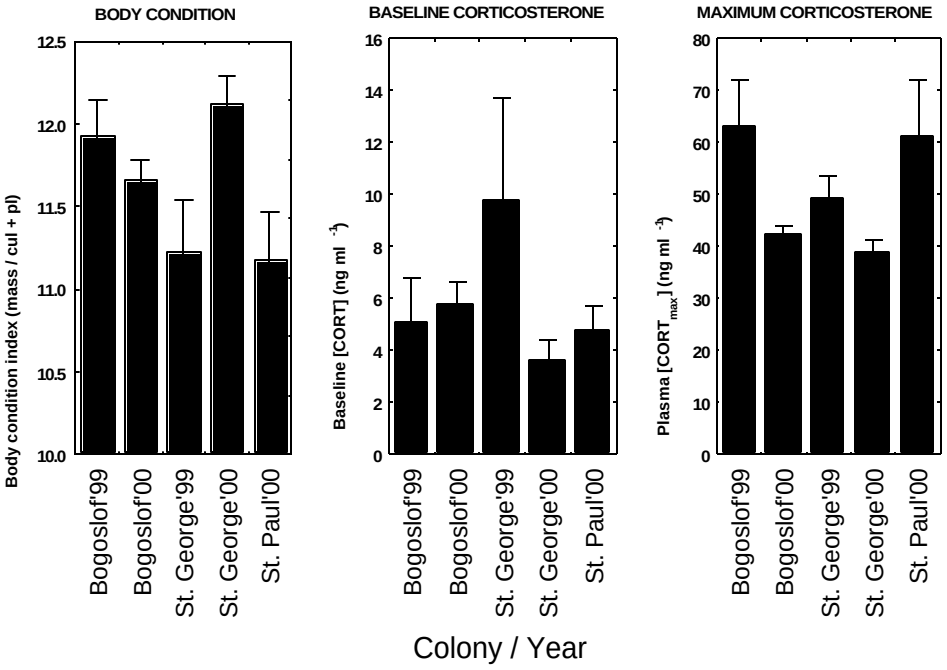
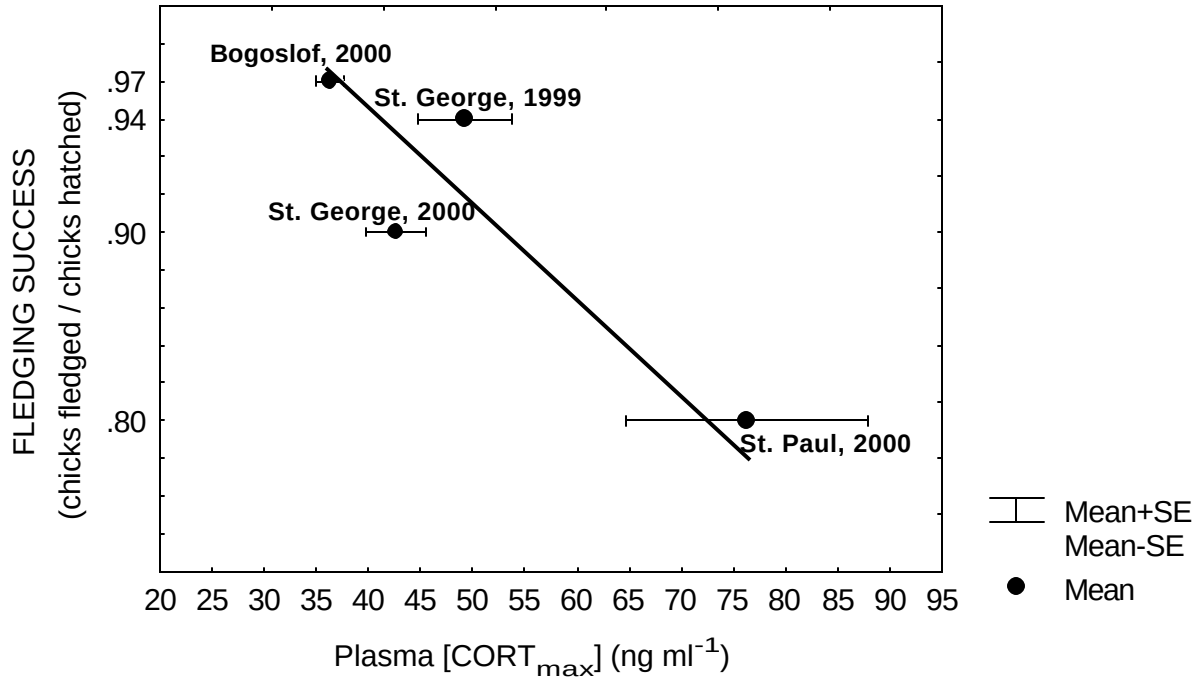


Fig. 5. The relationship between maximum levels of corticosterone at incubation and fledging success in common murres.

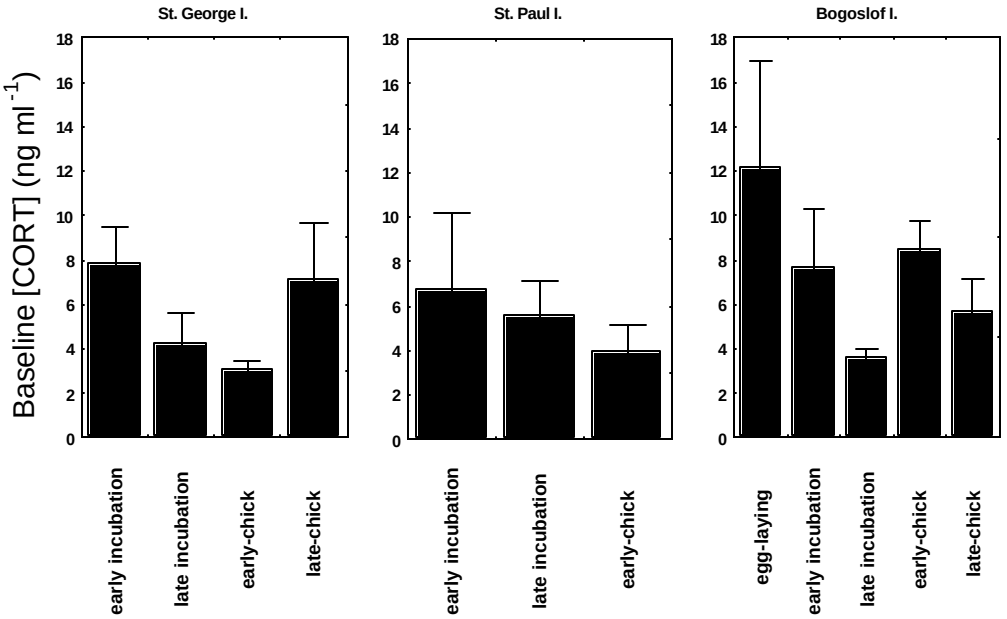


INTRA-SEASONAL COMPARISONS

Baseline levels of corticosterone

In 2000, baseline levels of corticosterone did not differ among the colonies ($F_{2, 100}$=0.812, p=0.447, Fig. 6) and tended to decline from early incubation to chick-rearing (reproductive stage effect: $F_{2, 100}$=2.97, p=0.056).

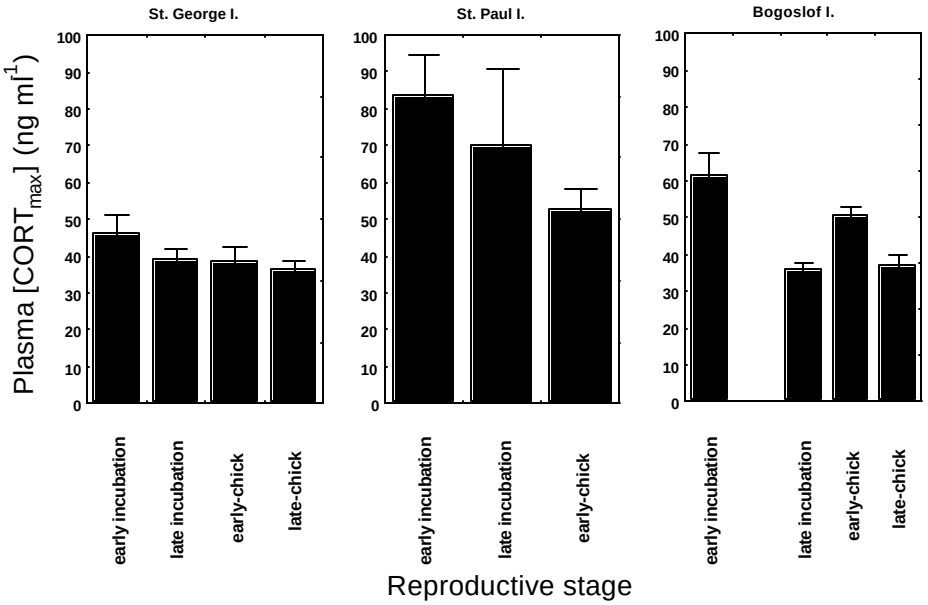
Fig. 6. Intra-seasonal dynamics of baseline corticosterone in common murres, Bering Sea 2000 (mean, SE)



Adrenocortical response to acute stress

In 2000, maximum levels of corticosterone achieved by common murres in response to acute stress of capture and restraint differed among the colonies ($F_{2, 91}$=14.78, p<0.00001, Fig. 7), and declined from early incubation to chick-rearing ($F_{2, 91}$=8.62, p<0.001). This seasonal trend was similar among the colonies (colony X reproductive stage interaction: $F_{4, 91}$=1.76, p=0.143). Maximum levels of corticosterone were higher in murres nesting at St. Paul I. compared to those in birds nesting at St. George (p<0.00001) and Bogoslof (p=0.0001) Islands.

Fig. 7. Intra-seasonal dynamics of maximum corticosterone in common murres, Bering Sea 2000 (mean, SE)



INTER-COLONY EFFECTS (comparisons between Bering Sea 1999-2000 at late-incubation - early-chick-rearing and Cook Inlet 1997-2000 at all stages)

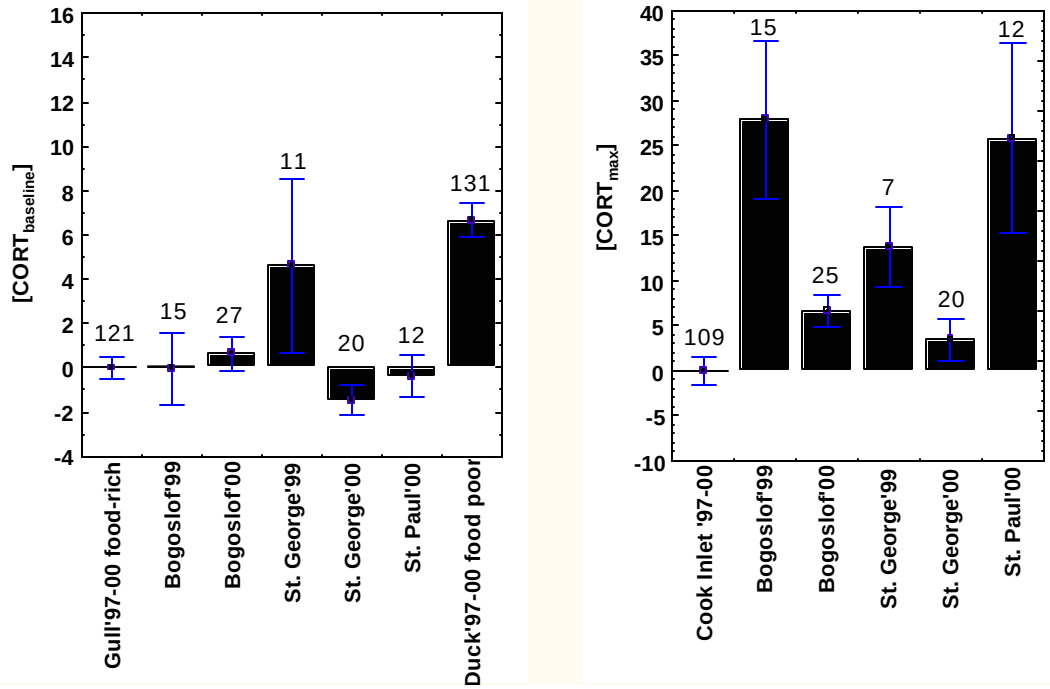
Baseline levels of corticosterone

Baseline levels of corticosterone varied significantly among common murre colonies in the Bering Sea and Cook Inlet ($F_{6, 330}$=11.21, p<0.000001, Fig. 8). Baseline levels of corticosterone in murres breeding at St. George in 1999 and Duck (food-poor colony) islands were significantly higher than those in birds breeding on Gull I. (food-rich colony). Common murres breeding at Bogoslof in 1999 and 2000, St. Paul in 2000 and St. George islands in 2000 were apparently not food limited during late-incubation – early chick-rearing (Fig. 8).

Adrenocortical response to acute stress

At late-incubation – early chick-rearing, maximum levels of corticosterone achieved by common murres in response to acute stress of capture and restraint were significantly different among the colonies ($F_{5, 182}$=9.28, p<0.00001, Fig. 8). Maximum levels of corticosterone in murres breeding at St. George, St. Paul and Bogoslof Islands in Bering Sea appeared to be higher than those in birds breeding in Cook Inlet (Gull and Duck Islands, 1997-2000, combined).

Fig. 8. Comparison of physiological parameters among common murres breeding in the southeastern Bering Sea and Cook Inlet (mean, SE) Data for food-rich Gull I. (baseline) and all combined data for Cook Inlet (for maximum levels) were used as 0-lines.



Adult attendance and provisioning

In 2000, common murres nesting on St. George I. had less loafing time than birds nesting on Bogoslof I. or colonies in Cook Inlet (Table 1). At the same time, frequency of foraging trips and trip duration were within a normal range observed for this species (Table 1). Other studies of common murres (e.g., Zador and Piatt 2000, and references therein) suggested that loafing time is one of the most sensitive behavioral parameters to variations in food availability. Accordingly, patterns of nest attendance by parent common murres in 2000 suggest that foraging conditions were favorable for the birds nesting on Bogoslof I. and sub-optimal for birds nesting at St. George I.

Table 1. Nest attendance patterns of chick-rearing Common Murres

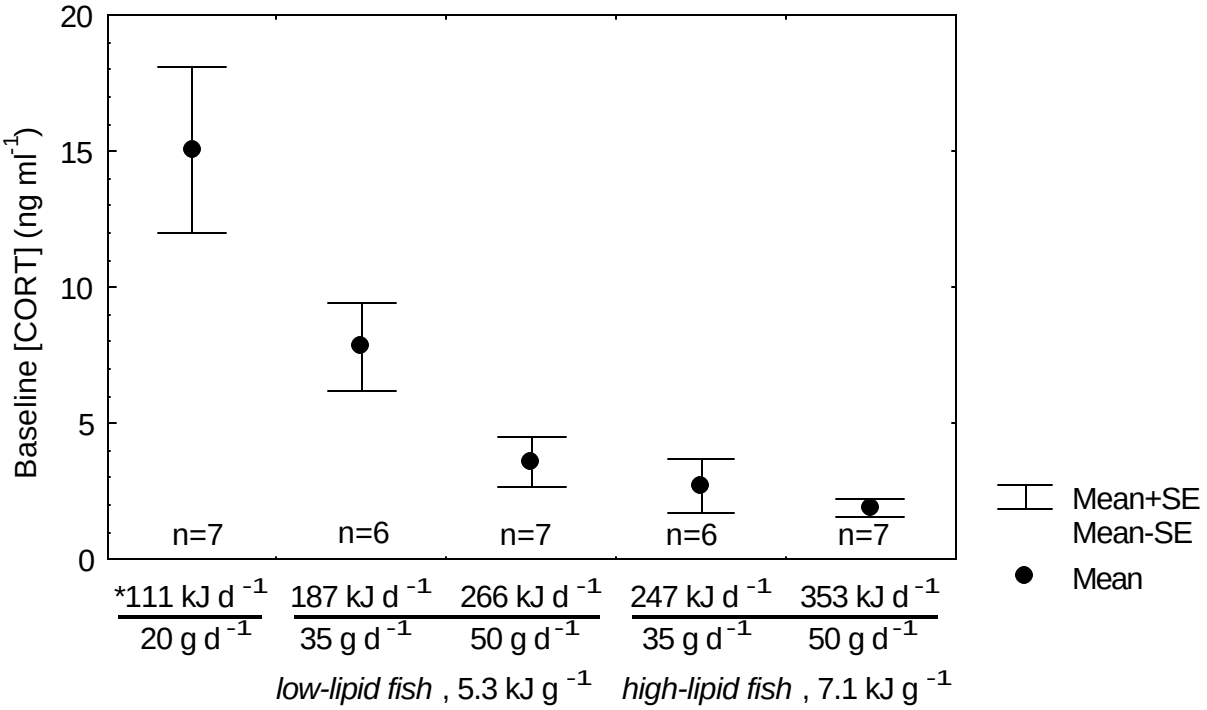
Colony, sample size	Year	# of foraging trips (trips · day^{-1})	Foraging trip duration (min · day^{-1})	Loafing time (%)
St. George, n=20	2000	4.5 (0.41)	177.9 (27.23) n=18	2.4 (0.28)
Bogoslof I., n=13	2000	2.5 (0.42)	247.5 (37.51) n=10	9.8 (3.96)
Duck I., n=92	1996-2000	2.8 (0.12)	220.2 (11.10) n=88	3.8 (0.73)
Gull I., n=57	1996-2000	3.4 (0.23)	137.4 (7.51) n=55	15.9 (1.63)

MURRE CHICKS

Captive experiment:

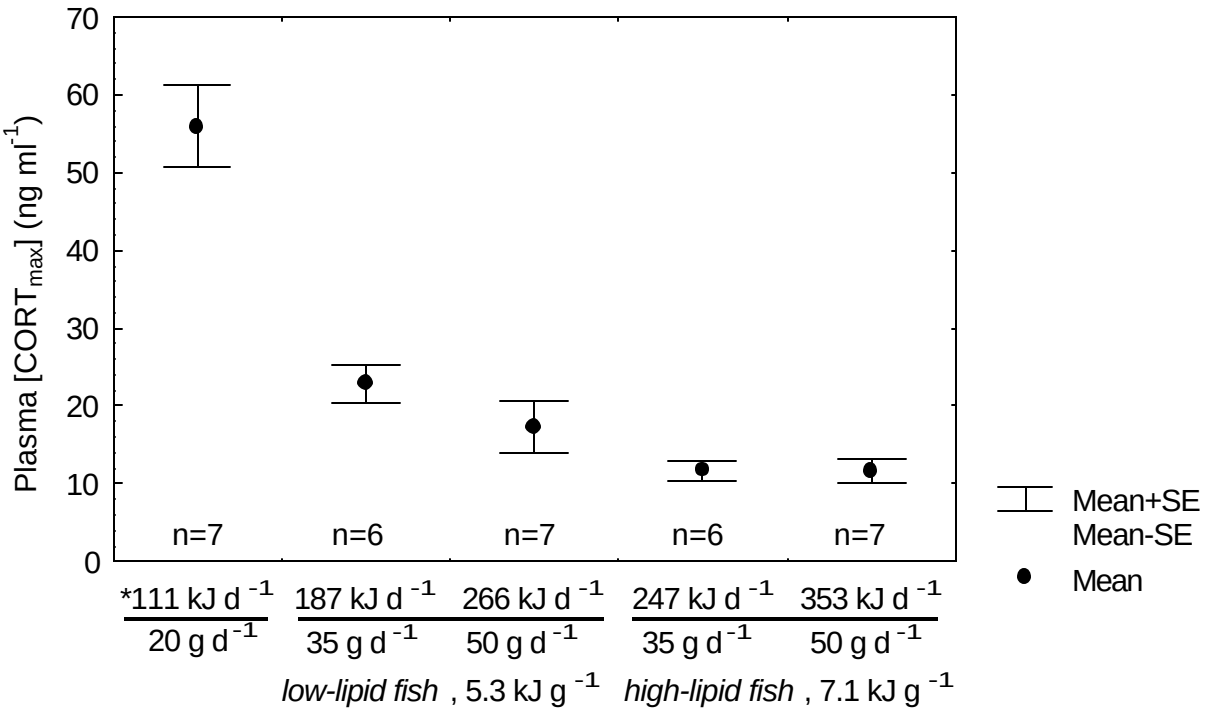
Dietary treatments had a significant effect on baseline levels of corticosterone in 4-week-old common murre chicks ($F_{4, 28}$=13.05, p=0.000004, Fig. 9). In particular, baseline levels were elevated in captive chicks that were fed a reduced amount (35 g d^{-1}) of a relatively low-lipid fish compared to chicks fed high-lipid fish given at 35 and 50 g d^{-1} (Fig. 9). Baseline levels were also elevated in ca. 4-week-old free-living chicks at a food-poor colony on Duck I. (marked with an asterisk on Fig. 9), which were fed by their parents at a relatively low rate, ca. ~20 g d^{-1} (calculation based on all-day (12 hrs) of observations at the colony in 2000, recorded food delivery rate 1.62 feeds hr^{-1} , estimated energy density of fish ~5.7 kJ g^{-1}).

Fig. 9. Baseline levels of corticosterone in 4-week-old common murre chicks in relation to daily energy intake.



Dietary treatments had a significant effect on maximum acute stress-induced levels of corticosterone in common murre chicks ($F_{4, 28}$=24.26, p<0.0001, Fig. 10). Similar to baseline levels, maximum levels of corticosterone were elevated in captive chicks that were fed a reduced amount (35 g d^{-1}) of low-lipid fish compared to chicks fed high-lipid fish at rates of 35 and 50 g d^{-1} (Fig. 10). Maximum levels were also elevated in ca. 4-week-old free-living chicks at Duck I., which were fed by their parents at a lower rate, ca.~20 g d^{-1} (Fig. 10).

Fig. 10. Maximum acute stress-induced levels of corticosterone in 4-week-old common murre chicks in relation to daily energy intake



Dietary treatments also had highly significant effects on growth and development of common murre chicks (for a detailed report of the results see attached manuscript by Benowitz-Fredericks and Kitaysky, in preparation).

Comparison of the adrenocortical response in common murre chicks and fledglings

We examined corticosterone levels in common murre chicks captured at the nest site (nestling) and in chicks that were captured after leaving the nest, en route to the ocean (fledglings). Baseline levels of corticosterone were higher in common murre fledglings compared to those in nestlings captured simultaneously at the same colony (Fig. 11). On the other hand, acute stress-induced levels of corticosterone (at 30 minutes of capture and restraint) were not statistically different between nestlings and fledglings ($F_{1, 16}$=0.37, p=0.553, Fig. 11). It is likely that murre chicks respond to the process of fledging (jumping off a cliff, following by a temporal separation from a parent) with an increase in secretion of corticosterone, which is similar to their response to an acute stressor of capture and restraint. Thus, corticosterone levels in fledglings might reflect their nutritional state (see the results of captive experiments above). For instance (Fig. 12), corticosterone levels in common murre fledglings at Duck I. (food-poor colony) were significantly higher than those in fledglings at Bogoslof I. in 2000 (colony effect: $F_{1, 29}$=7.07, p=0.013). Based on these logics, in 2000, common murre fledglings at Bogoslof I. were in better nutritional state than common murre fledglings at Duck I.

Fig. 11. Adrenocortical response of 2-4 week old common murre chicks to acute stress of capture and restraint, Duck I. 2000

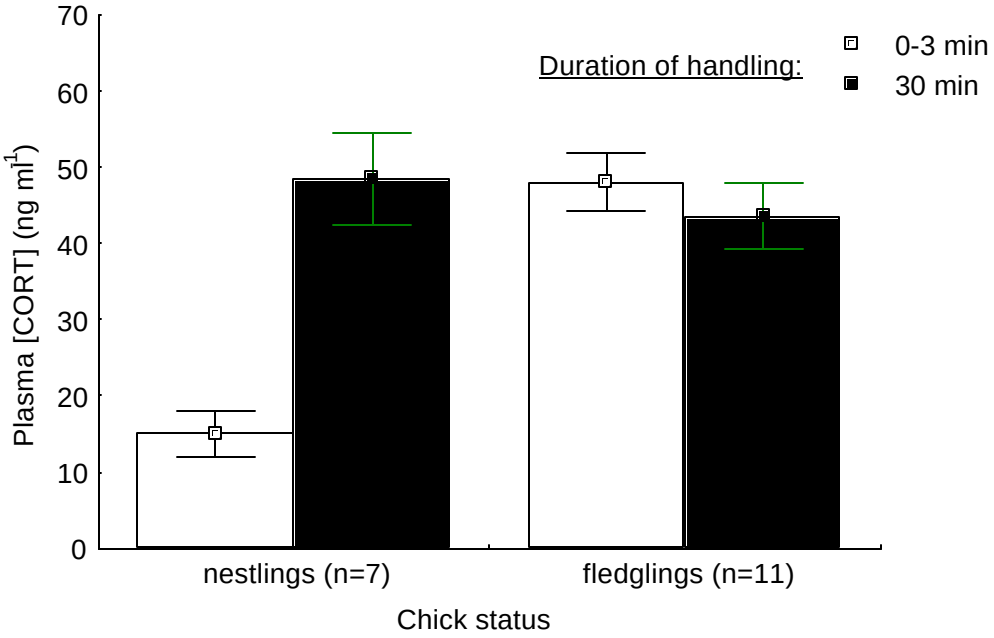
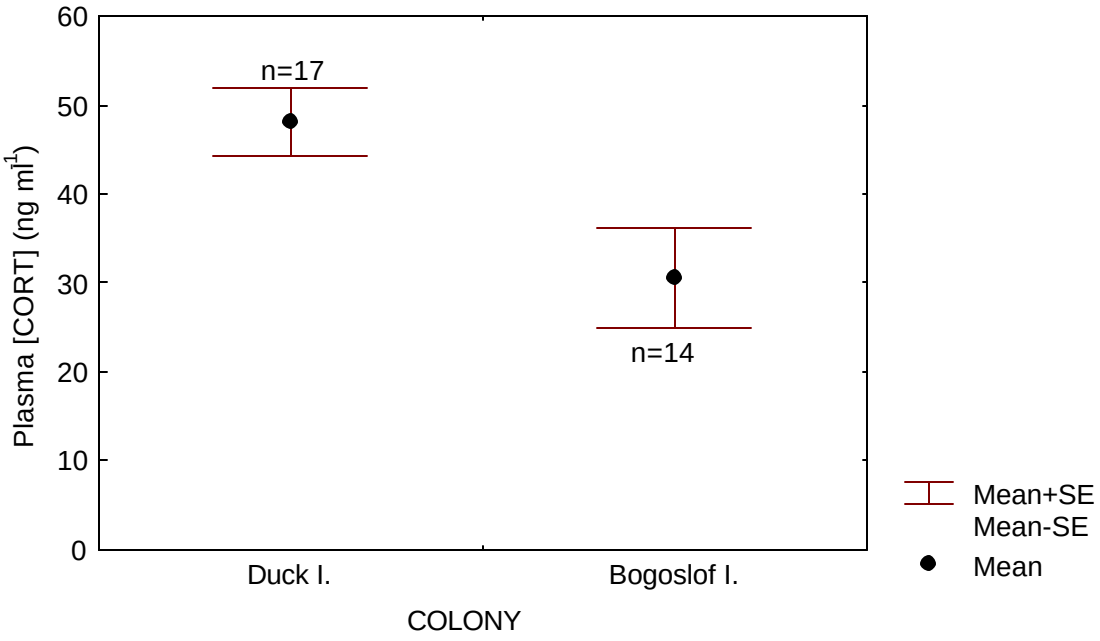


Fig. 12. Corticosterone levels in common murre fledglings, 2000 (blood samples were taken within 3 minutes after capture)



Conclusions for the common murre

Common murres were food-deprived in 1999 on St. George I. (as indicated in low body mass and elevated baseline levels of corticosterone). Common murres nesting at Bogoslof, St. Paul and St. George (in 2000) islands did not appear to be food-limited during early chick-rearing. Nevertheless, elevated acute stress-induced levels of corticosterone suggest that common murres could have been food-limited at earlier stages of reproduction at Bogoslof, St. Paul and St. George Islands in 1999 and in 2000. As reflected in baseline levels of corticosterone, fledglings of common murres nesting at Bogoslof I. were not nutritionally in 2000 stressed compared to chicks at Duck I. Overall, a comparison of the physiological parameters of common murres breeding in the Bering Sea with food-rich (Gull I.) and food-poor (Duck I.) colonies in Cook Inlet suggest that birds nesting at Pribilof and Bogoslof islands are more likely to be food-limited early in the season (upon arrival at the breeding colonies), but are not food-limited during egg-laying – chick-rearing stages of reproduction.

THICK-BILLED MURRES

INTER-ANNUAL COMPARISONS

Body condition

Body conditions of thick-billed murres during late-incubation were lower in 1999 than in 2000 (year effect: $F_{1, 72}$=11.83, p=0.001, Fig. 13). There was a significant colony effect ($F_{2, 72}$=13.28, p=0.00001): birds breeding at Bogoslof I. were lighter than birds breeding at St. George I. (LSD post-hoc, p=0.045) and at St. Paul I. (p<0.0001; birds breeding at St. George I. were lighter than birds breeding at St. Paul I. (p=0.009). These inter-colony patterns in adult murre body condition were similar in 1999 and 2000 (colony X year interaction term: $F_{2, 72}$=0.23, p=0.798, Fig. 13).

Baseline levels of corticosterone

Baseline levels of corticosterone during late-incubation were higher in 1999 than in 2000 (year effect: $F_{1, 69}$=29.16, p<0.0001, Fig. 13). Baseline levels of corticosterone also varied significantly among the colonies (colony effect: $F_{2, 69}$=10.3, p=0.0001), murres nesting at St. George I. had significantly higher baseline levels of corticosterone than murres nesting at Bogoslof (p=0.0001) and St. Paul (p=0.0004) islands. There was a significant year X colony interaction term ($F_{2, 69}$=6.09, p=0.004). In particular, baseline levels were significantly higher in 1999 than in 2000 at St. George (p<0.0001) and St. Paul (p=0.019), but did not change between the years at Bogoslof I. (p=0.269).

Adrenocortical response to acute stress

Maximum levels of corticosterone achieved by thick-billed murres in response to acute stress of capture and restraint were significantly higher in 1999 than in 2000 (year effect: $F_{1, 62}$=36.12, p<0.000001, Fig. 13). The year effect was similar among the colonies (colony effect: $F_{2, 62}$=0.64,

p=0.533; year X colony interaction term: $F_{2, 62}$=2.23, p=0.116). During late incubation, maximum levels of corticosterone were negatively correlated with the proportion of lipids in the colony/year-specific diet (beta= -0.42, R^2=.18, $F_{1, 56}$=12.19, p=0.001, Fig. 14).

Fig. 13. Inter-annual variability of physiological parameters in thick-billed murres at late-incubation, Bering Sea 1999-2000

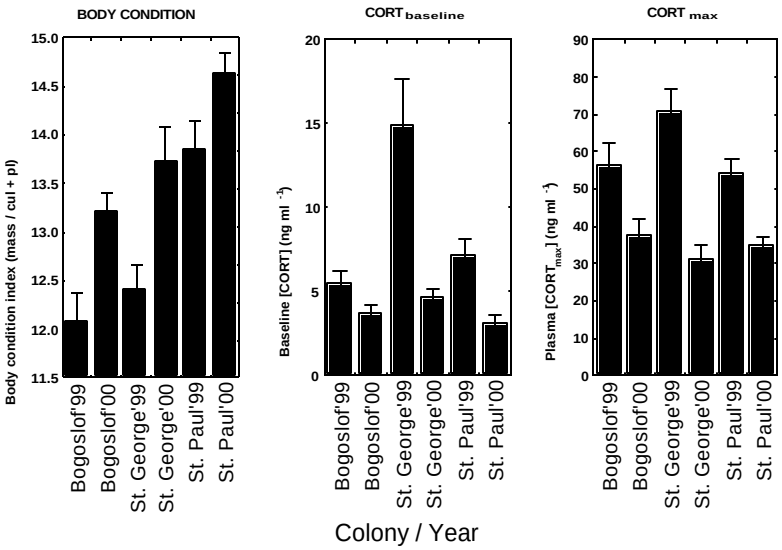
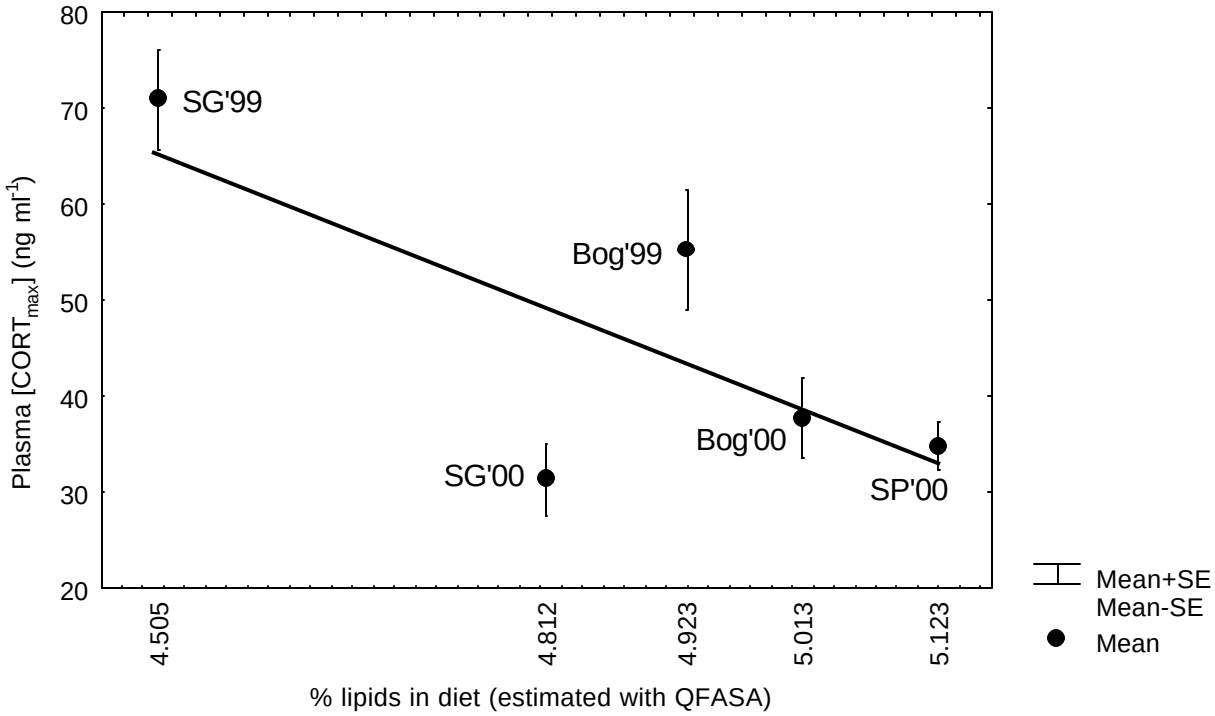


Fig. 14. The relationship between diet quality and maximum levels of corticosterone in thick-billed murres at late incubation

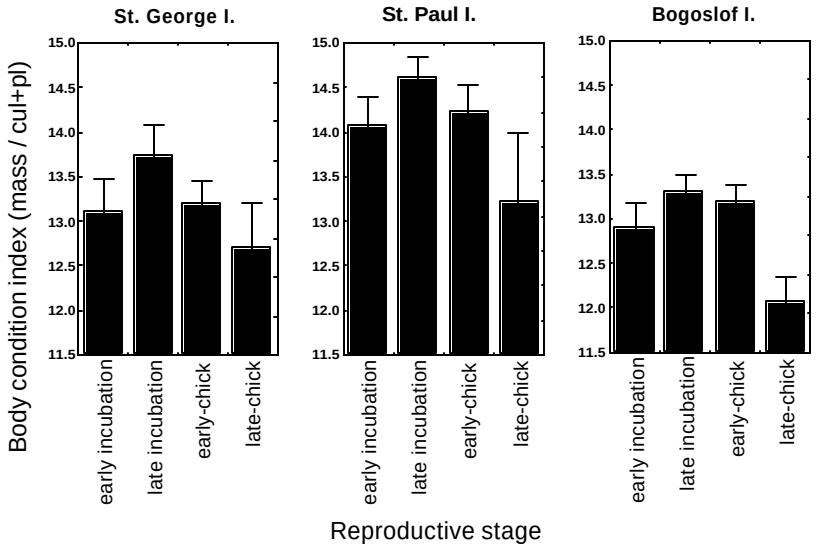


INTRASEASONAL EFFECTS

Body condition

In 2000, body condition of thick-billed murres declined between early-incubation and late chick-rearing (reproductive stage effect: $F_{3, 125}$=5.12, p=0.002, Fig. 15), and intra-seasonal changes in body condition were similar among the colonies (stage X colony interaction term: $F_{6, 125}$=0.99, p=0.436). Colony had a significant effect on body condition (colony effect: $F_{2, 125}$=5.43, p=0.006): birds were lighter at Bogoslof I. compared to St. George (p=0.045) and St. Paul (p=0.001) islands.

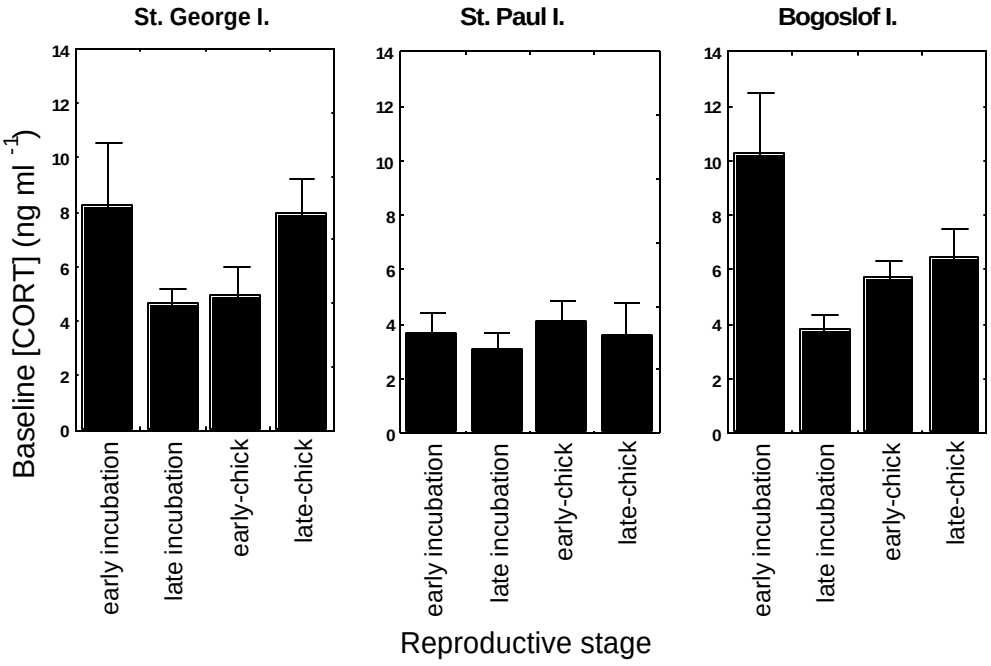
Fig. 15. Seasonal dynamics of body condition in thick-billed murres



Baseline levels of corticosterone

In 2000, baseline levels of corticosterone (Fig. 16) varied significantly among colonies ($F_{2, 117}$=6.24, p=0.003) and reproductive stages ($F_{3, 117}$=4.55, p=0.004), whereas intra-seasonal changes in baseline levels were similar among the colonies (colony X stage interaction term: $F_{6, 117}$=1.341, p=0.244). Baseline levels were lower in birds breeding at St. Paul I. compared to those in birds breeding at Bogoslof (p=0.003) and St. George (p=0.011) islands. Baseline levels of corticosterone were higher during early incubation than during late incubation (p<0.001) or early chick-rearing (p=0.015).

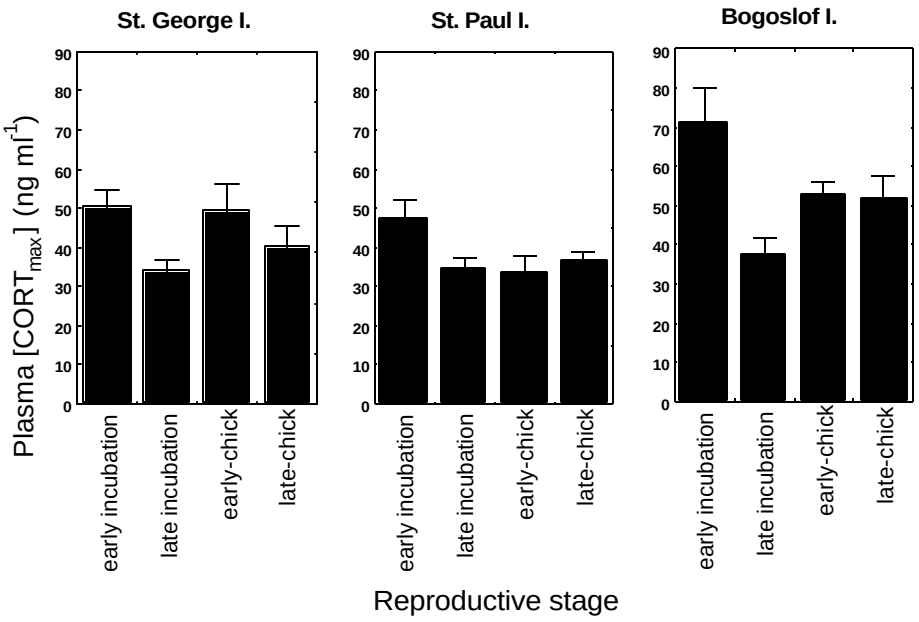
Fig. 16. Seasonal dynamics of baseline corticosterone in thick-billed murres



Adrenocortical response to acute stress

In 2000, maximum levels of corticosterone (Fig. 17) achieved by thick-billed murres in response to acute stress of capture and restraint differed among colonies ($F_{2, 115}$=8.97, p=0.0002), and among reproductive stages ($F_{3, 115}$=8.34, p=0.00005). Intra-seasonal variations in maximum levels of corticosterone were similar among colonies (colony X reproductive stage interaction: $F_{6, 115}$=1.29, p=0.266). Maximum levels of corticosterone were higher during early-incubation than during late incubation (p<0.00001), or during early- (p=0.009) and late-chick rearing (p=0.005). Maximum levels of corticosterone were higher in birds breeding at Bogoslof I. than in birds at St. Paul (p<0.0001) and St. George (p=0.010) islands.

Fig. 17. Seasonal dynamics of maximum corticosterone in thick-billed murres



Adult attendance and provisioning

In 2000, thick-billed murres nesting on St. George I. exhibited the last amount of loafing time, and fewer chick-feeding trips of longer duration than birds nesting at St. Paul and Bogoslof islands. Comparisons of adult attendance and provisioning between 2000 and late 1980s (Kitaysky et al. 2000) revealed a drastic change in behavior of birds nesting at St. Paul I. The number of foraging trips almost doubled and loafing time tripled in 2000, whereas duration of foraging trips was almost five times shorter than it was in 1987-1988 (Table 2).

Table 2. Nest attendance patterns of chick-rearing Thick-billed Murres

Colony, sample size	Year	# of foraging trips (trips · day^{-1})	Foraging trip duration (min · day^{-1})	Loafing time (%)
St. Paul, n=7	1987	2.5 (0.62)	272.9 (63.35)	6.6 (3.27)
St. Paul, n=8	1988	2.9 (0.46)	261.1 (40.07)	5.3 (1.34)
St. Paul, n=10	**2000**	**6.7 (2.82)**	**47.8 (13.31)[1]**	**21.2 (7.47)**
St. George, n=18	1987	5.9 (0.75)	162.0 (23.53)	7.8 (1.97)
St. George, n=16	1988	2.9 (0.43)	325.6 (66.18)	2.6 (0.62)
St. George, n=18	**2000**	**4.0 (0.43)**	**214.3 (32.80)[2]**	**4.0 (0.91)**
Bogoslof, n=12	**2000**	**4.2 (0.51)**	**171.1 (27.79)[3]**	**15.2 (4.36)**

[1]sample size n=7 (nests); [2] =17; [3]=11

Conclusions:

As indicated by poor body condition, and increased baseline and acute stress-induced levels of corticosterone1999 was a food-poor year for thick-billed murres breeding at all three colonies. As reflected in baseline levels of corticosterone, birds nesting at St. George I. were more strongly affected by food shortages in 1999 than birds at Bogoslof I. and St. Paul I. During food-rich 2000, foraging conditions were favorable for thick-billed murres on all three colonies, but birds nesting at St. Paul I. were in better physiological condition compared to birds nesting at Bogoslof and St. George islands. Colony attendance and rate of chick provisioning also suggest that murres nesting at St. Paul I. experienced much better foraging conditions than con-specifics nesting at St. George I. Finally, seasonal dynamics of body condition, baseline and acute stress-induced levels of corticosterone suggest that food was relatively scarce near colonies early in the season (probably upon arrival of thick-billed murres to the breeding colonies). Despite obvious inter-annual differences in food supply, breeding success of thick-billed murre did not change inter-annually (V. Byrd ReFER report) and was not correlated with physiological condition of parents (data are not shown).

BLACK-LEGGED KITTIWAKES

INTER-ANNUAL COMPARISON

Body mass

Body mass of adult black-legged kittiwakes at early chick-rearing was lower in 1999 than in 2000 (year effect: $F_{1, 48}$=10.08, p=0.003, Fig. 18). Birds breeding at Bogoslof I. were heavier than those at St. Paul I. (colony effect: $F_{1, 48}$=7.34, p=0.009). No data for inter-annual comparisons were obtained at St. George I.

Baseline levels of corticosterone

Baseline levels of corticosterone varied between colonies (colony effect: $F_{1, 48}$=6.80, p=0.012, Fig. 18), whereas differences in baseline levels between years were not statistically significant ($F_{1, 48}$=1.30, p=0.259). Birds breeding at St. Paul I. in 1999 had higher baseline levels compared to those in birds breeding at Bogoslof I. in 1999 and 2000 (p<0.03 for both years). Baseline levels of corticosterone (Fig. 19) were negatively correlated with colony/year-specific estimates of fledging success (beta= -.39, R^2=.15, $F_{1, 49}$=8.79, p=0.005)

Fig. 18. Interannual variations in physiological condition of black legged kittiwakes during early chick-rearing in 1999 and 2000

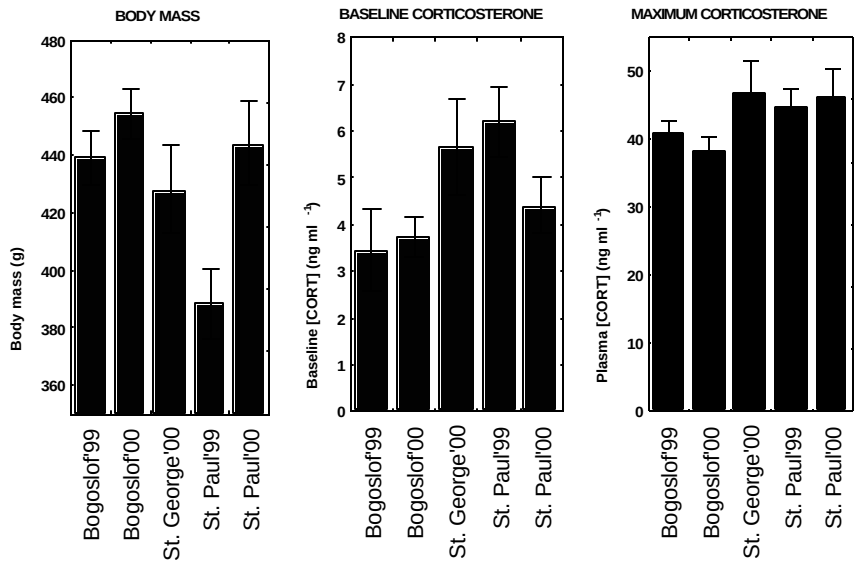
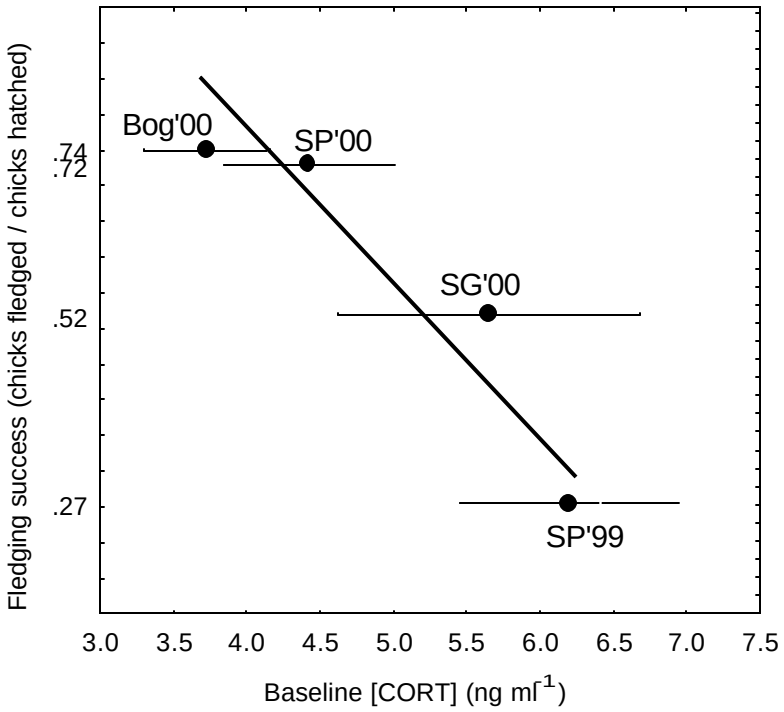


Fig. 19. The relationship between baseline levels of corticosterone at early chick-rearing and fledging success in black-legged kittiwakes



Adrenocortical response to acute stress

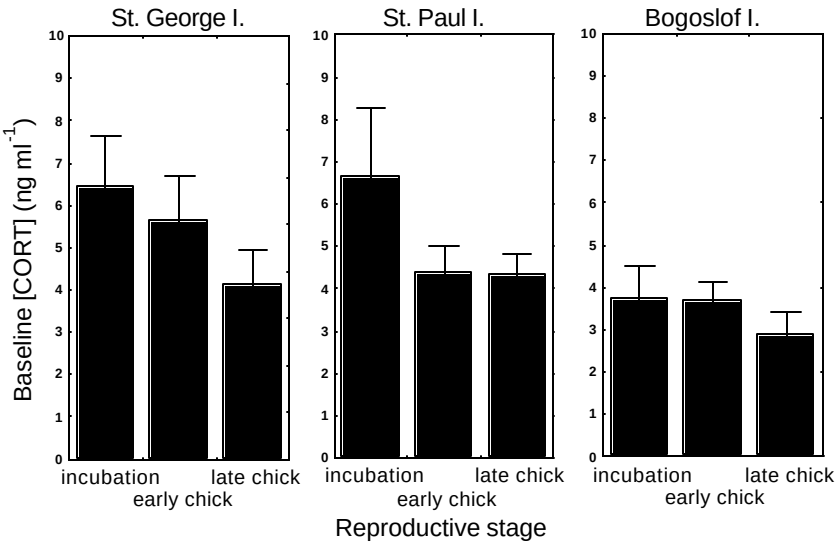
Maximum levels of corticosterone achieved by black-legged kittiwakes in response to acute stress of capture and restraint were similar among years (year effect: $F_{1, 39}$=0.04, p=0.839), and between colonies (colony effect: $F_{1, 39}$=3.21, p=0.081).

INTRASEASONAL EFFECTS

Baseline levels of corticosterone

In 2000, baseline levels of corticosterone (Fig. 20) differed among colonies ($F_{2, 99}$=3.87, p=0.024) and tended to decline from incubation to late chick-rearing (reproductive stage effect: $F_{2, 99}$=2.64, p=0.076). Baseline levels of corticosterone were lower in birds nesting at Bogoslof I. than in birds nesting at St. George (p=0.014) and at St. Paul (p=0.026) islands.

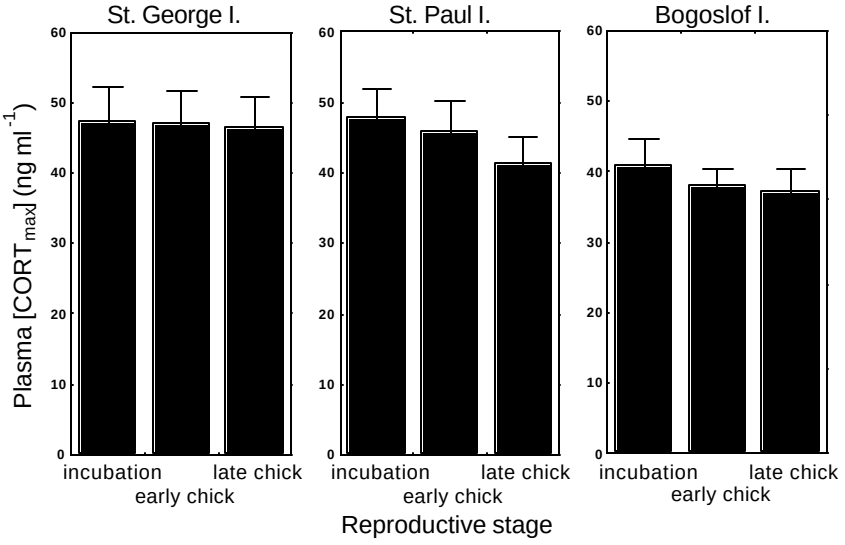
Fig. 20. Seasonal dynamics of baseline corticosterone in black-legged kittiwakes in the Bering Sea during 2000



Adrenocortical response to acute stress

In 2000, maximum levels of corticosterone achieved by black-legged kittiwakes in response to acute stress of capture and restraint differed among colonies ($F_{2, 94}$=3.73, p=0.028, Fig. 21), but did not differ among reproductive stages ($F_{2, 94}$=0.64, p=0.529). Maximum levels of corticosterone were lower in kittiwakes nesting at Bogoslof I. than in birds nesting on St. George (p=0.011) and St. Paul (p=0.042) islands.

Fig. 21. Seasonal dynamics of maximum corticosterone in black-legged kittiwakes in the Bering Sea during 2000

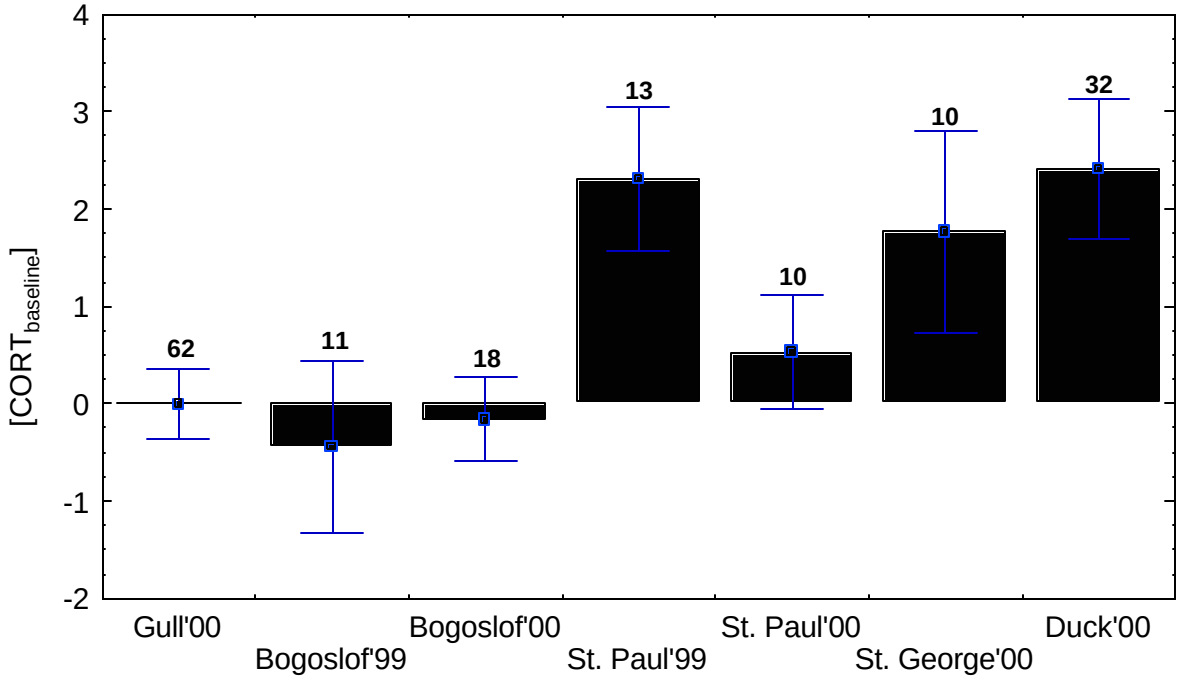


INTER-COLONY EFFECTS (comparisons between Bering Sea 1999-2000 and Cook Inlet 2000)

Baseline levels of corticosterone

During late-incubation – early chick-rearing, baseline levels of corticosterone (Fig. 22) varied among black-legged kittiwake colonies in the Bering Sea and Cook Inlet ($F_{6, 149}$=3.29, p=0.005). Baseline levels of corticosterone in kittiwakes breeding at St. George and St. Paul Islands tended to be similar to those in birds breeding at Duck I. (food-poor colony), whereas baseline levels of birds at Bogoslof I. were more similar to those of kittiwakes breeding at Gull I. (food-rich colony).

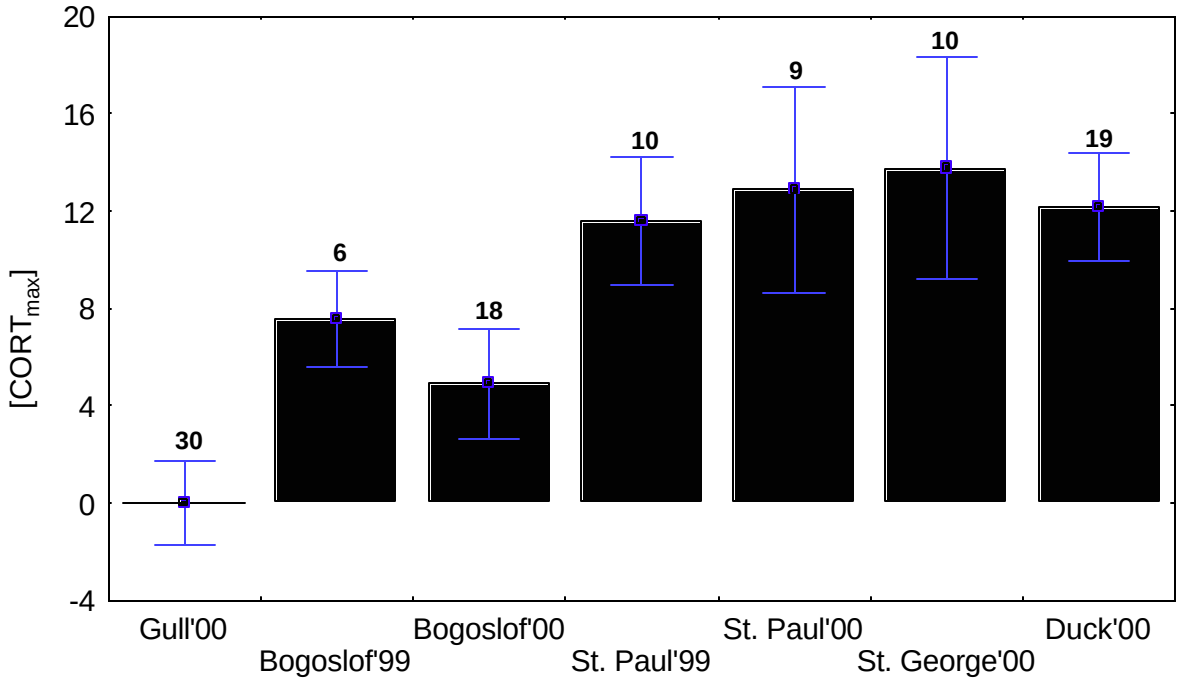
Fig. 22. Inter-colony comparison of baseline levels of corticosterone in black-legged kittiwakes during 1999-2000. Data for Gull I. used as a 0-line.



Adrenocortical response to acute stress

During late-incubation – early chick-rearing, maximum levels of corticosterone (Fig. 23) achieved by black-legged kittiwakes in response to acute stress of capture and restraint differed among colonies ($F_{6, 95}$=4.71, p=0.0003). Maximum levels of corticosterone in kittiwakes breeding at St. George and St. Paul Islands were similar to those in birds breeding at Duck I. (food-poor colony), whereas maximum levels in birds breeding at Bogoslof I. were intermediate between those in kittiwakes breeding at Gull I. (food-rich colony) and Duck I.

Fig. 23. Inter-colony comparison of maximum levels of corticosterone in black-legged kittiwakes during 199-2000. Data for Gull I. used as a 0-line.



Adult attendance and provisioning

In 2000, chicks of black-legged kittiwakes nesting on St. George I. were left unattended by their parents for much longer periods ever recorded at colonies in Cook Inlet (Table 3). Earlier observations of black-legged kittiwakes at the Pribilof Islands in 1987-88 (Kitaysky et al. 2000; Table 3) suggest that this type of behavior is typical for black-legged kittiwakes during food shortages. At the same time, other behavioral parameters: trip duration and frequency were within a range of values recorded for black-legged kittiwakes breeding at Pribilof Islands during the late 1980s and more recently in Cook Inlet (Table 3).

Table 3. Nest attendance patterns of chick-rearing Black-legged Kittiwakes

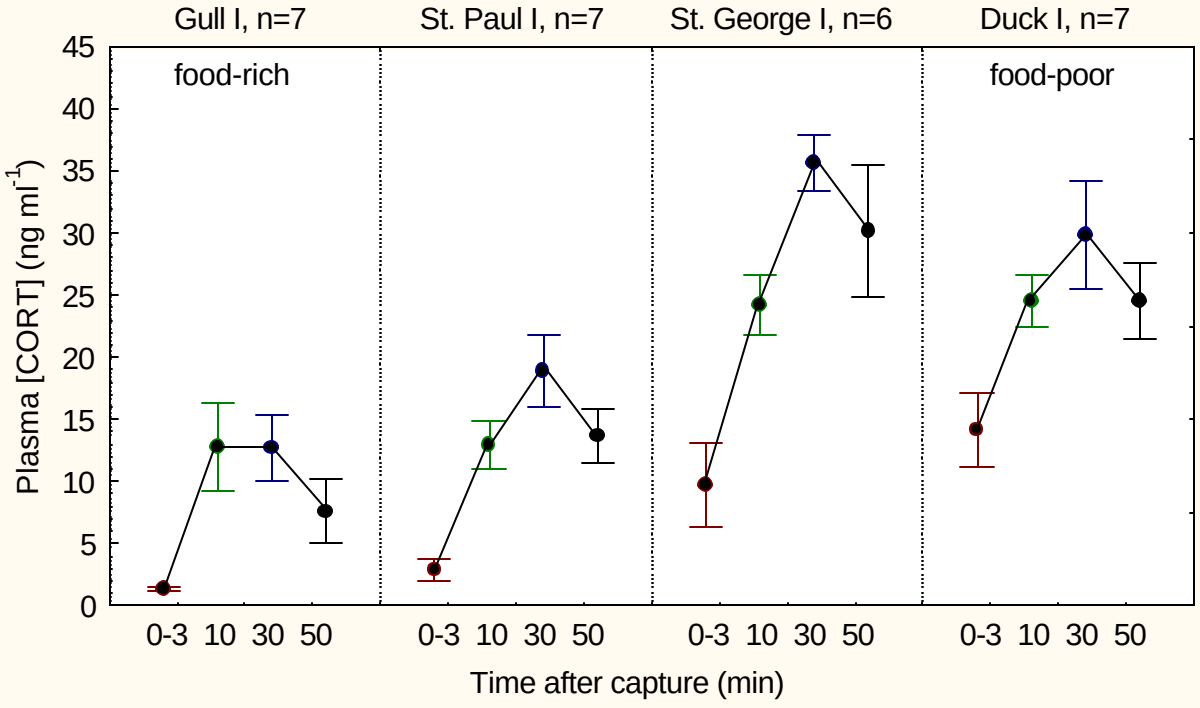
Colony, sample size	Year	# of foraging trips (trips · day^{-1})	Foraging trip duration (min · trip^{-1})	Time chicks spent alone (%)
St. Paul, n=5	1987	1.8 (0.35)	673.1 (131.59)	39.5 (5.10)
St. Paul, n=11	1988	2.7 (0.30)	289.7 (23.42)	0.1 (0.08)
St. George, n=5	1988	3.2 (0.31)	235.9 (20.18)	0
St. George, n=8	2000	2.5 (0.79)	250.5 (42.65)[1]	52.1 (15.29)
Duck I., n=23	1996-1997	1.7 (0.65)	293.9 (30.54)[2]	3.9 (1.73)
Gull I., n=121	1996-2000	3.0 (0.14)	207.4 (10.56)[3]	1.4 (0.56)

[1] sample size n=5; [2]n=30, [3]n=107.

BLACK-LEGGED KITTIWAKE CHICKS

Baseline levels of corticosterone in 5 week-old black-legged kittiwake chicks (Fig. 24) differed among colonies in 2000 ($F_{3, 25}$=6.17, p=0.0003). In particular, baseline levels (at 0-3 min after capture) were elevated in kittiwake chicks at St. George I. and Duck I. (food-poor colony) compared to chicks at Gull I. (food-rich colony) and St. Paul I. The adrenocortical stress responses were also higher in chicks at St. George and Duck islands than in chicks at food-rich Gull I. (colony effect: $F_{3, 23}$=16.01, p=0.00001, duration of handling: $F_{3, 69}$=29.22, p<0.00001; colony X handling interaction term: $F_{3, 69}$=1.21, p=0.304). Baseline and adrenocortical response to acute stress in chicks at St. Paul I. were similar to those in chicks at food-rich Gull I. (Fig. 24).

Fig. 24. Adrenocortical response of 5-week old, singleton, black-legged kittiwake chicks to acute stress.



Conclusions for black-legged kittiwakes:
As indicated by low body mass and elevated baseline levels of corticosterone, 1999 was a food-poor year for black-legged kittiwakes on St. Paul I. Black-legged kittiwakes nesting at Bogoslof I. did not appear to be food-limited during early chick-rearing in either 1999 or 2000. Nevertheless, elevated acute stress-induced levels of corticosterone suggest that black-legged kittiwakes might have been food-limited at earlier stages of reproduction at Bogoslof and St. Paul islands in 1999, and at St. Paul and St. George Islands in 2000. As reflected in baseline levels and acute stress-induced of corticosterone, chicks of black-legged kittiwakes nesting at St. George I. in 2000 were nutritionally stressed compared to chicks at St. Paul I. Overall, a comparison of the physiological parameters among black-legged kittiwakes breeding in the Bering Sea with food-rich (Gull I.) and food-poor (Duck I.) colonies in Cook Inlet suggest that birds nesting at Pribilof Islands are more likely to be food-limited than birds nesting at Bogoslof I. Finally, seasonal dynamics of acute stress-induced levels of corticosterone suggest that food shortages are more likely to occur near all three colonies early in the season (upon arrival of red-legged kittiwakes to the colonies and during egg-laying – early incubation stages of reproduction).

RED-LEGGED KITTIWAKES

INTER-ANNUAL COMPARISONS

Body mass

Body mass of adult red-legged kittiwakes during early chick-rearing (Fig. 25) was lower in 1999 than in 2000 (year effect: $F_{1, 46}$=12.35, p=0.001). Colony effect was not significant (colony effect: $F_{2, 46}$=1.64, p=0.205), and inter-annual changes in body mass were similar among the colonies (colony X year interaction term: $F_{2, 46}$=3.04, p=0.057).

Baseline levels of corticosterone

Baseline levels of corticosterone (Fig. 26) varied among colonies (colony effect: $F_{2, 46}$=4.93, p=0.012), baseline levels of corticosterone were higher in red-legged kittiwakes breeding at St. George I. than in birds breeding at Bogoslof (p=0.005) and St. Paul (p=0.019) islands. There was a significant year X colony interaction term ($F_{2, 46}$=4.98, p=0.011). In particular, baseline levels were higher in 1999 than in 2000 at St. George (p<0.001), but there were no significant inter-annual differences in baseline levels at St. Paul and Bogoslof islands (Fig. 26).

Adrenocortical response to acute stress

Maximum levels of corticosterone achieved by red-legged kittiwakes in response to acute stress of capture and restraint were higher in 1999 than in 2000 (year effect: $F_{1, 30}$=20.32, p=0.0001, Fig. 26). The year effect was similar among the colonies (year X colony interaction term: $F_{2, 30}$=1.74, p=0.193). Colony did not have an effect on maximum levels of corticosterone ($F_{2, 30}$=0.57, p=0.571). During early chick-rearing, maximum levels of corticosterone (Fig. 27) were

significantly negatively correlated (beta= -0.68, R^2=0.46, $F_{1, 24}$=20.33, p=0.0002) with the proportion of lipids in the colony/year-specific diets (as estimated with QFASA model, see Springer and Iverson ReFER report for details). Maximum levels of corticosterone were also negatively correlated with the productivity (beta= -0.68, R^2=0.45, $F_{1, 34}$=28.29, p<0.00001, Fig. 28).

Fig. 26. Inter-annual comparison of physiological condition of red-legged kittiwakes during early chick-rearing, 1999-2000

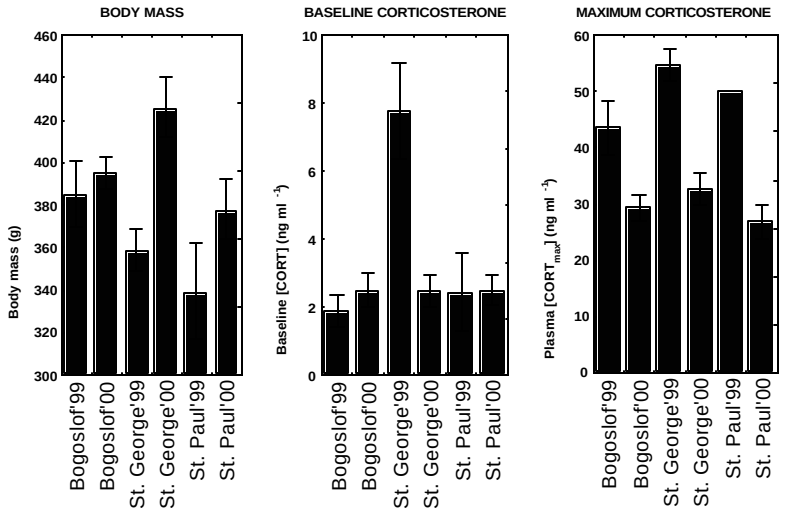


Fig. 27. The relationship between diet quality and maximum levels of corticosterone in red-legged kittiwakes during early chick-rearing

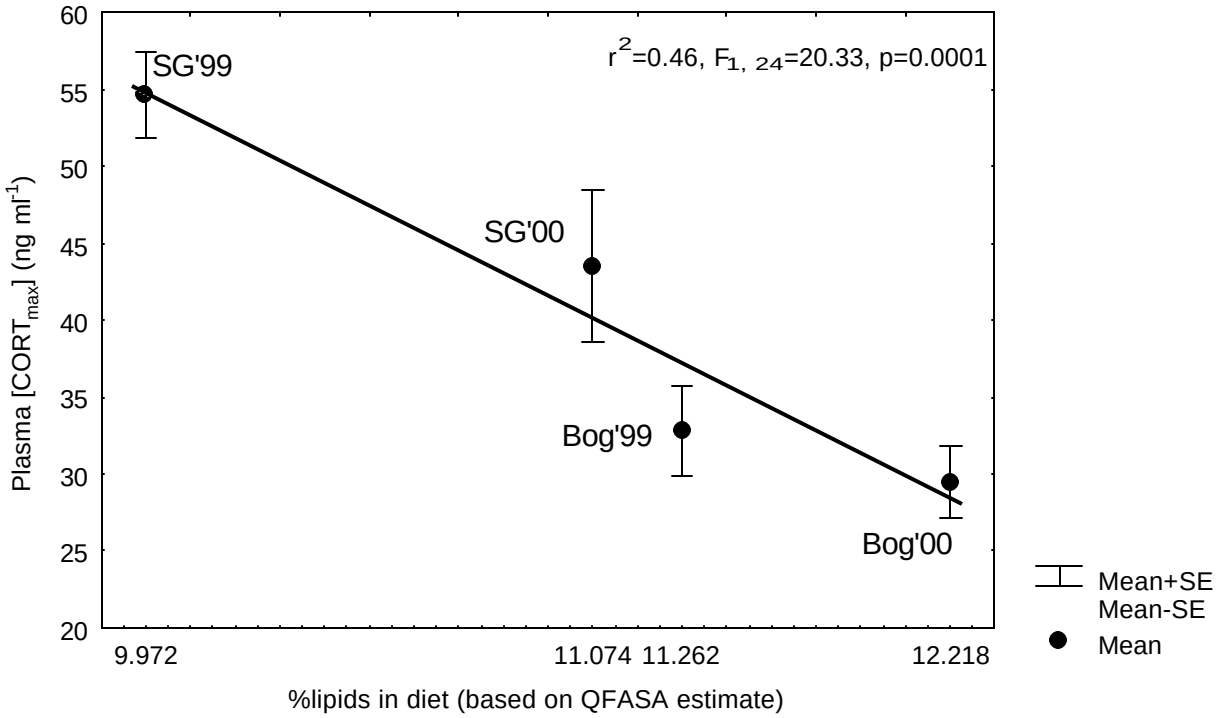
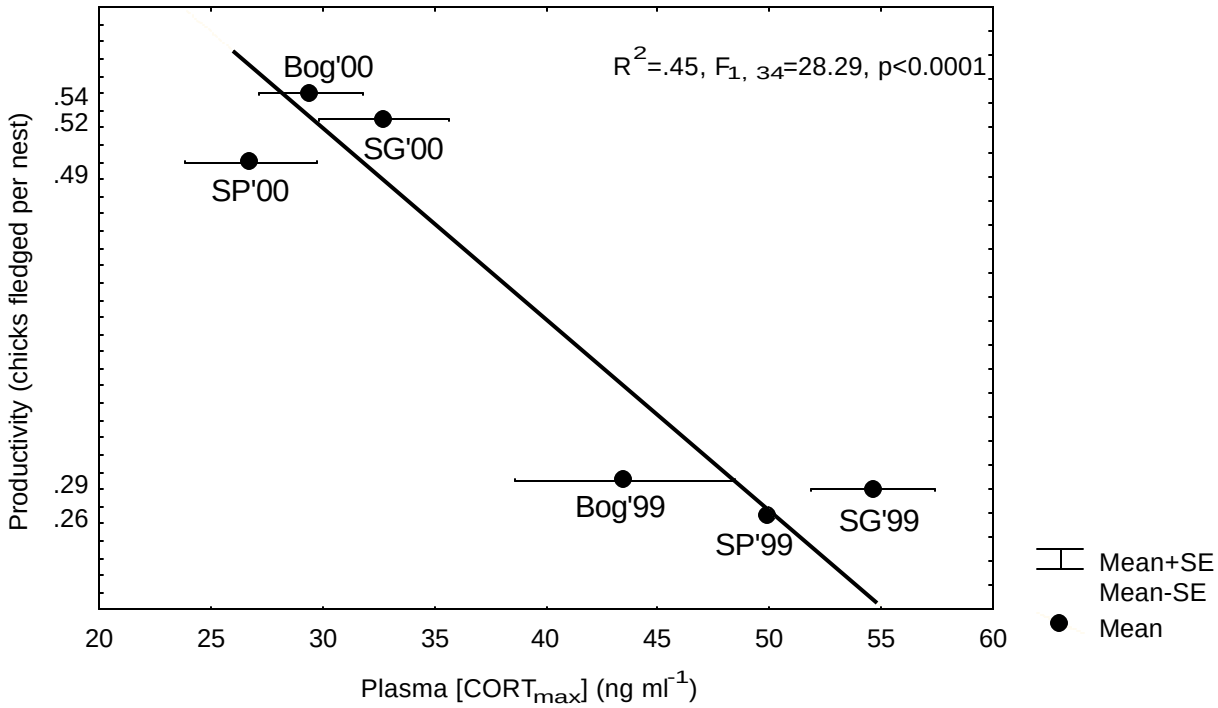


Fig. 28. The relationship between productivity and maximum levels of corticosterone in red-legged kittiwakes during early chick-rearing

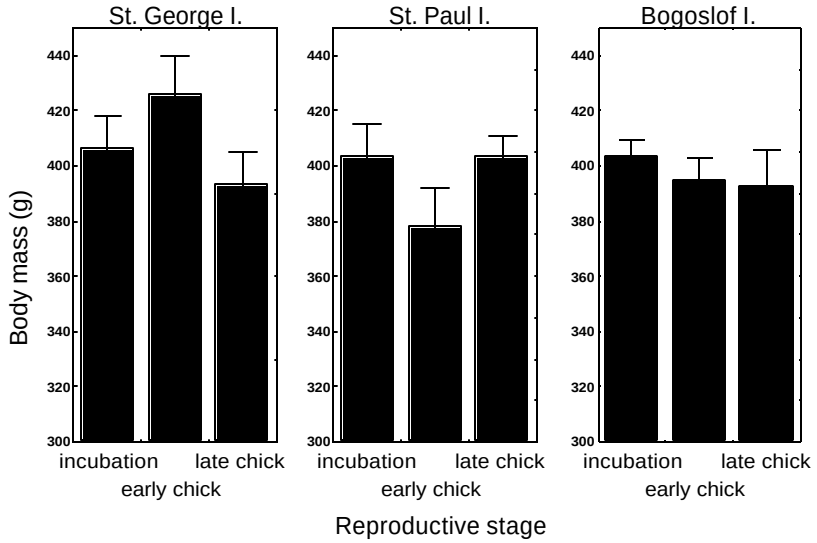


INTRASEASONAL EFFECTS

Body mass

In 2000, body mass of red-legged kittiwakes (Fig. 29) changed little between early-incubation and late chick-rearing (reproductive stage effect: $F_{2, 107}$=0.38, p=0.688), and intra-seasonal dynamics of body mass were similar among colonies (stage X colony interaction term: $F_{4, 107}$=1.595, p=0.181). Body mass of kittiwakes did not differ among colonies ($F_{2, 107}$=1.105, p=0.335).

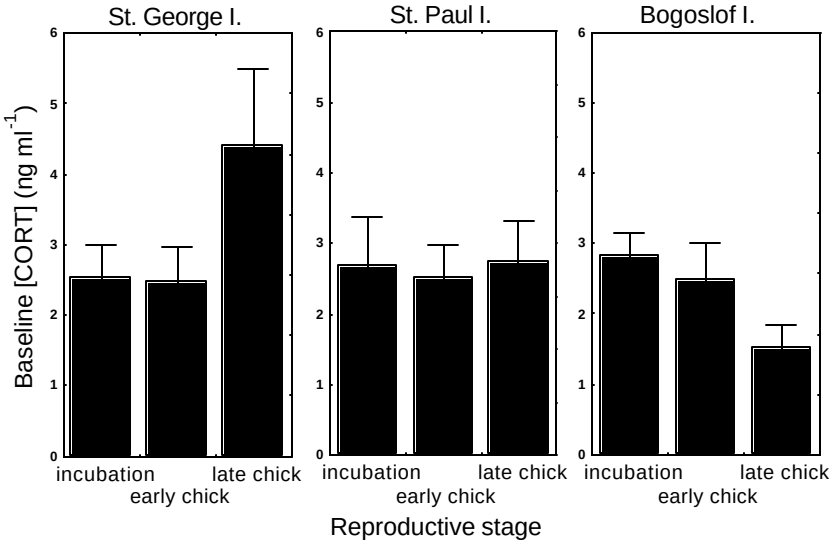
Fig. 29. Seasonal changes in body mass of red-legged kittiwakes during 2000.



Baseline levels of corticosterone

In 2000, baseline levels of corticosterone (Fig. 30) were similar among colonies ($F_{2, 107}$=1.45, p=0.240) and reproductive stages ($F_{2, 107}$=0.26, p=0.769), and intra-seasonal changes in baseline levels were similar among colonies (colony X stage interaction term: $F_{4, 107}$=1.888, p=0.118).

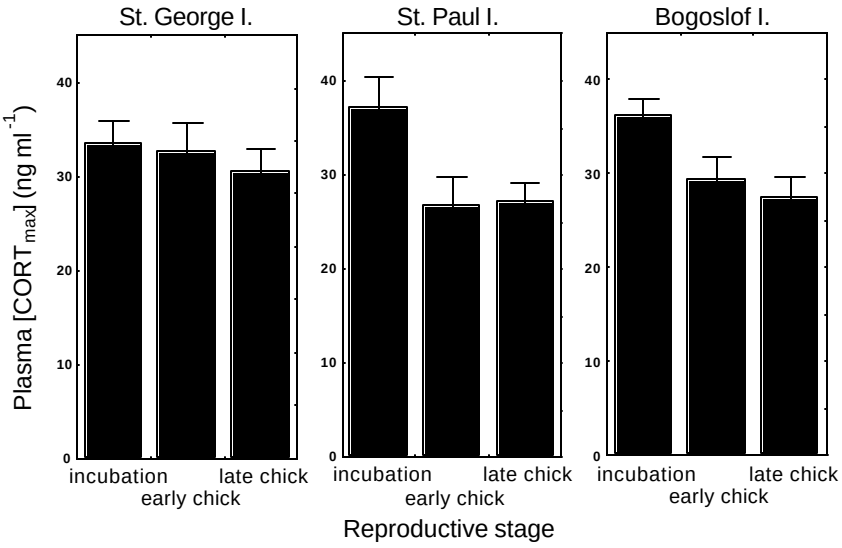
Fig. 30. Seasonal changes in baseline levels of corticosterone in red-legged kittiwakes during 2000.



Adrenocortical response to acute stress

In 2000, maximum levels of corticosterone (Fig. 31) achieved by red-legged kittiwakes in response to acute stress of capture and restraint did not differ among colonies ($F_{2, 91}$=0.35, p=0.708), and intra-seasonal dynamics of maximum levels of corticosterone were similar among colonies ($F_{4, 91}$=0.91, p=0.463). However, maximum levels of corticosterone declined throughout the reproductive season (reproductive stage effect: $F_{2, 91}$=6.45, p=0.002). Maximum levels of corticosterone were higher at incubation than at early chick-rearing (p=0.009) or late-chick rearing (p=0.002).

Fig. 31. Seasonal dynamics of maximum corticosterone in red-legged kittiwakes during 2000.



Adult attendance and provisioning

Nest attendance by red-legged kittiwakes at St. George I. in 2000 appeared to be similar to earlier observations in 1988 (Kitaysky et al. 2000) (Table 4).

Table 4. Nest attendance patterns of chick-rearing Red-legged Kittiwakes

Colony, sample size	Year	Feeding rate (feeds · hr^{-1})	Foraging trip duration (min · $trip^{-1}$)	Time chicks spent alone (%)
St. George, n=5	1988	-	362.8 (72.03)	0
St. George, n=10	2000	0.13 (0.02)	319.0 (100.74)*	2.1 (2.1)

*n=7

RED-LEGGED KITTIWAKE CHICKS

Results of the experimental study of the adrenocortical stress response in red-legged kittiwake chicks in relation to nutritional stress revealed that chicks of red-legged kittiwakes respond to food shortages by increasing secretion of corticosterone (Kitaysky et al. 2001, attached). Furthermore, chicks of red-legged kittiwakes breeding at St. George I. in 2000 experienced physiological stress (Kitaysky et al. 2001). However, whether this stress was caused by the lack of nutrients or by infestation with ticks (or by a combination of two) was not resolved (Kitaysky et al. 2001). It was difficult to interpret the results because elevated corticosterone secretion and high tick infestation might be associated with nutritional stress. Regardless of causal factors, chronically elevated levels of corticosterone during early development might have long-lasting effects on a bird's quality later in life (see below), and this may have caused a decrease in post-fledging survival of red-legged kittiwakes raised on St. George I. in 2000.

A captive experimental study of the effects of nutritional stress during development on cognitive abilities of red-legged kittiwakes later in life provided evidence that even a short episode of stress during early development might permanently damage a bird's ability to learn foraging techniques. Consequently, nutritional stress might decrease its future survival (see manuscript in preparation, attached). In particular, results suggest that kittiwake chicks born during food-poor seasons might suffer inferior cognitive abilities and, therefore, would be less likely to survive after fledging. Thus, an estimate of reproductive success based on number of chicks fledged is likely to provide an inaccurate assessment of kittiwake recruitment in later years. Furthermore, individual red-legged kittiwakes affected by nutritional stress during early development may not be under-developed morphologically (which makes it difficult to detect nutritional stress in the field with traditional methods), yet they may have very different survival prospects compared to individuals that never experienced nutritional stress.

Conclusions for red-legged kittiwakes:

As indicated in low body mass, baseline and acute stress-induced levels of corticosterone, 1999 was a food-poor year for red-legged kittiwakes on all three colonies. As reflected in baseline levels of corticosterone, birds nesting at St. George I. were affected more strongly by food shortages than birds at Bogoslof and St. Paul islands. During relatively food-rich 2000, foraging conditions were favorable for red-legged kittiwakes breeding on all three colonies, but chicks of red-legged kittiwake nesting at St. George I. were in poor physiological condition compared to red-legged kittiwake chicks fed high-quality food *ad libitum* (see attached Kitaysky et al. 2001). Finally, seasonal dynamics of acute stress-induced levels of corticosterone suggest that food shortages are more likely to occur near all three colonies early in the season (upon arrival of red-legged kittiwakes to the colonies and during egg-laying – early incubation stages of reproduction).

OVERALL CONCLUSIONS

Are seabirds food-limited during reproduction? Previous studies suggest that food availability has been a major factor limiting reproductive performance of seabirds in the southeastern Bering Sea (Springer 1992; Decker et al. 1995; Hunt et al. 1996; Kitaysky et al. 2000). In order to test this hypothesis, we applied a physiological technique that directly measures food-related stress in seabirds. As indicated by the physiological parameters measured in four species of piscivorous seabirds breeding in the south-eastern Bering Sea, we conclude that 1999 was a relatively food-poor year, whereas 2000 was a relatively food-rich year. In particular, low poor body conditions and elevated levels of corticosterone were found in both species of murres and kittiwakes at late-incubation – early chick-rearing in 1999 compared to 2000. Furthermore, corticosterone levels and reproductive performance were negatively correlated in both species of kittiwakes and in the common murre. Overall, our study provides strong evidence that food availability is a major factor limiting reproduction of seabirds in the southeastern Bering Sea.

Is quality of food a limiting factor? Significant negative correlations between corticosterone levels and diet quality (determined with QFASA estimate of %-lipid in diets) in both species of murres and red-legged kittiwakes suggest that availability of fatty fishes to parent seabirds might be an important factor determining overall foraging success. These preliminary field results are strongly supported by the controlled experiments with captive birds showing that seabirds are capable of extracting more energy from diets high in lipids than from iso-caloric diets that are low in lipids (Romano 1999), and that the adrenocortical response of seabirds to nutritional deficit is exacerbated by low lipid content of their diets (Kitaysky et al. 1999, 2001; and the results of captive experiments reported here).

When do food shortages occur? As reflected in the physiological parameters measured in this study, inter-annual variability was a major component of temporal fluctuations in food availability. However, intra-seasonal changes in adrenocortical function point to the early stages of reproduction as a time period when kittiwakes and murres breeding in the southeastern Bering Sea are most likely to be food-limited. In addition, the adrenocortical response of incubating common murres to an acute stress of capture and restraint (as an indicator of food abundance in a previous month, see Fig. 1) was higher than we ever recorded during a long-term study of common murres breeding under wide range of foraging conditions in Cook Inlet. Furthermore, the patterns of seasonal declines of maximum corticosterone levels were similar among colonies and species in the Bering Sea. On the other hand, baseline levels of corticosterone (as an indicator of current food availability, see Fig. 1) also declined seasonally in 2000 suggesting that foraging condition improved markedly between early and late stages of reproduction for common murres and black-legged kittiwakes.

Which colonies are more strongly affected by food shortages? Seabirds breeding on the Pribilof Islands suffered more from food shortages in 1999 than did their con-specifics breeding on Bogoslof I. Specifically, elevated levels of corticosterone indicated that thick-billed and common murres, and red-legged kittiwakes, breeding on St. George I. were more severely affected by food shortages in 1999 than their con-specifics breeding on Bogoslof I. Black-legged kittiwakes breeding on St. Paul I. were also in poorer physiological condition (as reflected in low body mass and elevated corticosterone levels) than their con-specifics breeding on Bogoslof I. Based on these results, we conclude that if foraging conditions in the south-eastern Bering Sea are poor, seabirds breeding on the Pribilof Islands are likely to be more affected than their con-specifics breeding on Bogoslof I.

In 2000, black-legged kittiwakes breeding on the Pribilof Islands were in poorer physiological condition (as reflected in elevated baseline and acute stress-induced levels of corticosterone) than black-legged kittiwakes breeding on Bogoslof I. Also, chicks of red-legged and black-legged kittiwakes breeding on St. George I. in 2000 showed signs of physiological stress (elevated baseline and acute-stress induced levels of corticosterone) that are indicative of food-shortages (Kitaysky et al. 1999b, 2001b). Furthermore, baseline levels of corticosterone were elevated in chick-rearing red-legged kittiwakes at St. George I., whereas there was no indication of a seasonal increase in baseline levels in red-legged kittiwakes breeding on Bogoslof I. Finally, acute stress-induced levels of corticosterone were elevated in common murres breeding on St. Paul compared to those in common murres breeding on Bogoslof I. However, these indications of a better physiological condition of birds breeding on Bogoslof I. compared to Pribilof Islands in 2000 were relatively minor compared to inter-colony differences in 1999, and were not observed at all in thick-billed murres and adult red-legged kittiwakes. Thus, differences in physiological condition of birds breeding on Bogoslof and Pribilof Islands are likely to be less pronounced during seasons of relatively good foraging conditions.

Taken together, evidence suggests that food is more readily available to seabirds around Bogoslof than the Pribilofs, and this may explain why populations of seabirds increased during the previous 20+ years at Bogoslof, but have declined over a similar period at the Pribilofs.

Acknowledgements.
Field data were collected by the following people: Bogoslof (1999)-- Bob Adamcik, Catherine Berg, Karen Boylan, Vernon Byrd, Joel Gay, Alexander Kitaysky, Rosa Meehan, John Piatt, Bruce Robson, and Jeff Williams; Bogoslof (2000)-- Judy Alderson, Vernon Byrd, Sarah Iverson, Jared Figurski, Mayumi Arumitsu, Dean Kildaw, Alexander Kitaysky, Cliff Lascink, Rosa Meehan, Alan Springer, and Jeff Williams; St. George (1999)–Shelly DeNike, Dean Kildaw, Grace Merculief, Rachael Schindler, and Scott Taube; St. George (2000)– Stacey Buckelew, Kenneth Burton, Alexander Kitaysky, Gerald Masolini, Lori Ness, Nora Rojek, Art Sowls, Kent Sundseth, Connie Schwitters, Mike Schwitters, and Stephanie Toussaint; St. Paul I. (1999) – Dean Kildaw, Art Sowls, Tanya Bittner; and St. Paul I. (2000) – Tanya Bittner, Stacey Buckelew, Alexander Kitaysky, Nokolai Konyukhov, Mike Shultz, and Art Sowls. Captive experiments were conducted by Zhenya Kitaiskaia, Morgan Benowitz-Fredericks, Kindree Brownbridge, Roman Kitaysky, Alexander Kitaysky. Laboratory analyses were performed by Zhenya Kitaiskaia, Morgan Benowitz-Fredericks, Alexander Kitaysky, and John Wingfield. We

are grateful to the captain and crew of the M/V Tiglax for support and transportation. The project was made possible by funds and logistic support from the North Pacific Marine Research Program at the University of Alaska Fairbanks; The Alaska Science Center (USGS); The Alaska Maritime NWR (USFWS); the University of Washington; and the Exxon Valdez Oil Spill Trustee Council (Restoration Projects 01479, 01163M).

LITERATURE CITED

Anderson, P.J., and Piatt J.F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Mar. Ecol. Prog. Ser. 189:117-123.

Axelrod, J., and Reisine, T.D. 1984. Stress hormones: their interaction and regulation. *Science*, 23:355-365.

Burger, A.E., and Piatt, J.F. 1990. Flexible time budgets in breeding common murres: buffers against variable prey abundance. *Stud. Avian Biol*., 14:71-83.

Decker, MB., Hunt G.L., Byrd G.V. 1995. The relationships among sea-surface temperature, the abundance of juvenile walley pollock (Theragra chalcogramma) and the reproductive performance and diets of seabirds at the Pribiof Islands, southeastern Bering Sea. Can. Spec. Publ. Fish. Aquat Sci 121:425-437.

Hunt, G.L., Kitaysky A.S., Decker M.B., Dragoo D.E., and Springer A.M. Changes in the distribution and size of juvenile pollock, Theragra chalcogramma, as indicated by seabird diets at the Pribilof Islands, and by bottom trawl surveys in the eastern Bering Sea, 1975 to 1993. NOAA Tech. Rep. Ser., 126:133-147.

Hunt, G.L., M.B. Decker, and A.S. Kitaysky. 1996. Fluctuations in the Bering Sea ecosystem as reflected in the reproductive ecology and diets of kittiwakes on the Pribilof Islands, 1975-1991. Pp. 142-153 in: *Aquatic Predators and Their Prey*, Greenstreet, S.P.R. and M.L. Tasker (eds.). Fishing New Book, Oxford, England.

Hunt, G.L., and Byrd V.G. 1999. Marine bird populations and carrying capacity of the eastern Bering Sea. in Dynamics of the Bering Sea (eds. Louphlin T.R. and Ottani K.) 631-650 (Univ. of Alaska Sea Grant, Fairbanks, AK)

Kitaysky, A.S., Kitaiskaia E.V., Piatt J.F., & Wingfield J.C. benefits and costs of increased levels of corticosterone in seabird chicks. Horm. Behav., in press.

Kitaysky A.S., J.C. Wingfield, and J.F. Piatt. 1999*a*. Dynamics of food availability, body condition and physiological stress response in breeding kittiwakes. *Functional Ecology*, Vol. 13(5):577-584.

Kitaysky A.S., G.L. Hunt, E.N. Flint, M.A. Rubega, and M.B. Decker. 2000. Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Mar. Ecol. Prog. Ser.* 206:283-296.

Kitaysky A.S., J.C. Wingfield, and J.F. Piatt. 2001. Corticosterone facilitates begging and affects resource allocation in the Black-legged Kittiwake. *Behavioral Ecology*. 12:619-625.

Kitaysky A.S., J.F. Piatt, J.C. Wingfield, and M. Romano. 1999*b*. The adrenocortical stress-response of Black-legged Kittiwake chicks in relation to dietary restriction. *J. Comp. Physiol. B*, 169:303-310.

Kitaysky A.S., Kitaiskaia E.V., J.C. Wingfield, and J.F. Piatt. 2001*b*. Dietary restriction causes chronic elevation of corticosterone and enhances stress response in red-

legged kittiwake chicks. *J. Comp. Physiol. B*, 171:701-709.

Kitaysky A.S. 1999. Metabolic and developmental response of alcid chicks to variation in food availability. Physiol. Biochem. Zool. 72:469-473.

Kitaysky A.S., and Golubova E. 2000. Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. J. Anim. Ecol. 69:248-262.

Lloyd, C.S. 1979. Factors affecting breeding of Razorbills *Alca torda* on Skokholm. *Ibis*, 121:165-176.

Merrick, R.L., T.R. Loughlin, and Calkins, D.G. 1987. Decline in abundance of the northern sea lion, *Eumetopias jubatus*, in Alaska, 1956-86. *Fishery Bulletin* 85:351-365.

Øyan, H.S. and Anker-Nilssen, T. 1996. Allocation of growth in food-stressed Atlantic puffin chicks. *Auk*, 113(4):830-841.

Piatt, J.F. (ed.). 2002. Response of seabirds to fluctuations in forage fish density. Final Report to *Exxon Valdez* Oil Spill Trustee Council (Restoration Project 00163M) and Minerals Management Service (Alaska OCS Region). Alaska Science Center, U.S. Geological Survey, Anchorage, Alaska. 406 pp.

Piatt, J.F., and Anderson, P.J. 1996. Response of Common Murres to *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem. *In*: *Exxon Valdez* oil spill symposium proceedings (Rice, S.D., R.B. Spies, D.A. Wolfe, and Wright B.A., eds.). Amer. Fish. Society Symp. No 18.

Romano, M.D. 2000. Effects of diets on growth and development of nestling seabirds. MS Thesis, Oregon State University, Corvallis.

Sapolsky, R.M., L.C. Krey, and McEwen, B.S. 1986. The neuroendocrinology of stress and aging: the glucocorticosteroid cascade hypothesis. *Endocrine Reviews.* 7:284-301.

Sapolsky, R.M. 1987. Stress, social status, and reproductive physiology in free-living baboons. Pp. 291-322. *In*: Psychobiology of reproductive behavior: an evolutionary perspective (Crews D. ed.). Prentice hall, Englewood Cliffs, N.J.

Shea, R.E. and Ricklefs, R.E. 1996. Temporal variation in growth performance in six species of tropical, pelagic seabirds. *J. Anim. Ecol.*, 65:29-42.

Springer, A.M. 1992. A review: walley pollock in the North Pacific – how much difference do they make? Fish Oceanography, 1:80-96.

Thompson, P.M. and J.C. Ollason. 2001. Lagged effects of ocean climate change on fulmar population dynamics. Nature 413:417-420.

Wingfield, J.C., and Farner, D.S. 1980. Control of seasonal reproduction in temperate-zone birds. *Prog. Reprod. Biol*. 5:62-101.

Wingfield, J.C., C.M. Vleck, and Moore, M.C. 1992. Seasonal changes of the adrenocortical response to stress in birds of the Sonoran Desert. J. Exp. Zool. 264:419-428.

Wingfield, J.C., and Farner, D.S. 1976. Avian endocrinology - field investigations and methods. Condor 78:570-573.

Zador S.G., and Piatt J.F. 1999. Time-budgets of common murres at a declining and increasing colony in Alaska. Condor 101:149-152.